

PALEONTOLOGY IN THE GRAND CANYON OF ARIZONA:
125 YEARS OF LESSONS AND ENIGMAS FROM THE LATE PRECAMBRIAN
TO THE PRESENT

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Abstract

The Grand Canyon has been explored and studied by geologists since 1858. Fossils from the Canyon comprise a remarkably diverse collection; groups include late Precambrian microfossils and Paleozoic invertebrates, vertebrates, and plants. Trace fossils occur throughout the Canyon's stratigraphic sequence, including vertebrate and invertebrate trackways preserved in Pennsylvanian and Permian rocks. Late Cenozoic vertebrate and plant fossils are known from deposits near and within the Canyon. Interesting pseudofossils also are found throughout the strata, with some particularly problematical ones in the late Precambrian rocks. Many of the Grand Canyon's fossils have contributed to the development of geologic principles and to general interpretations of paleobiology. Today, the Grand Canyon may be an active agent in the evolution of some local species of land animals. But despite the tremendous amount of information that has been collected and interpreted from the Grand Canyon's long paleontological story, some areas of study have been sadly neglected, not so much from disinterest or lack of questions as from academic perplexity about the uniqueness of some of the material.

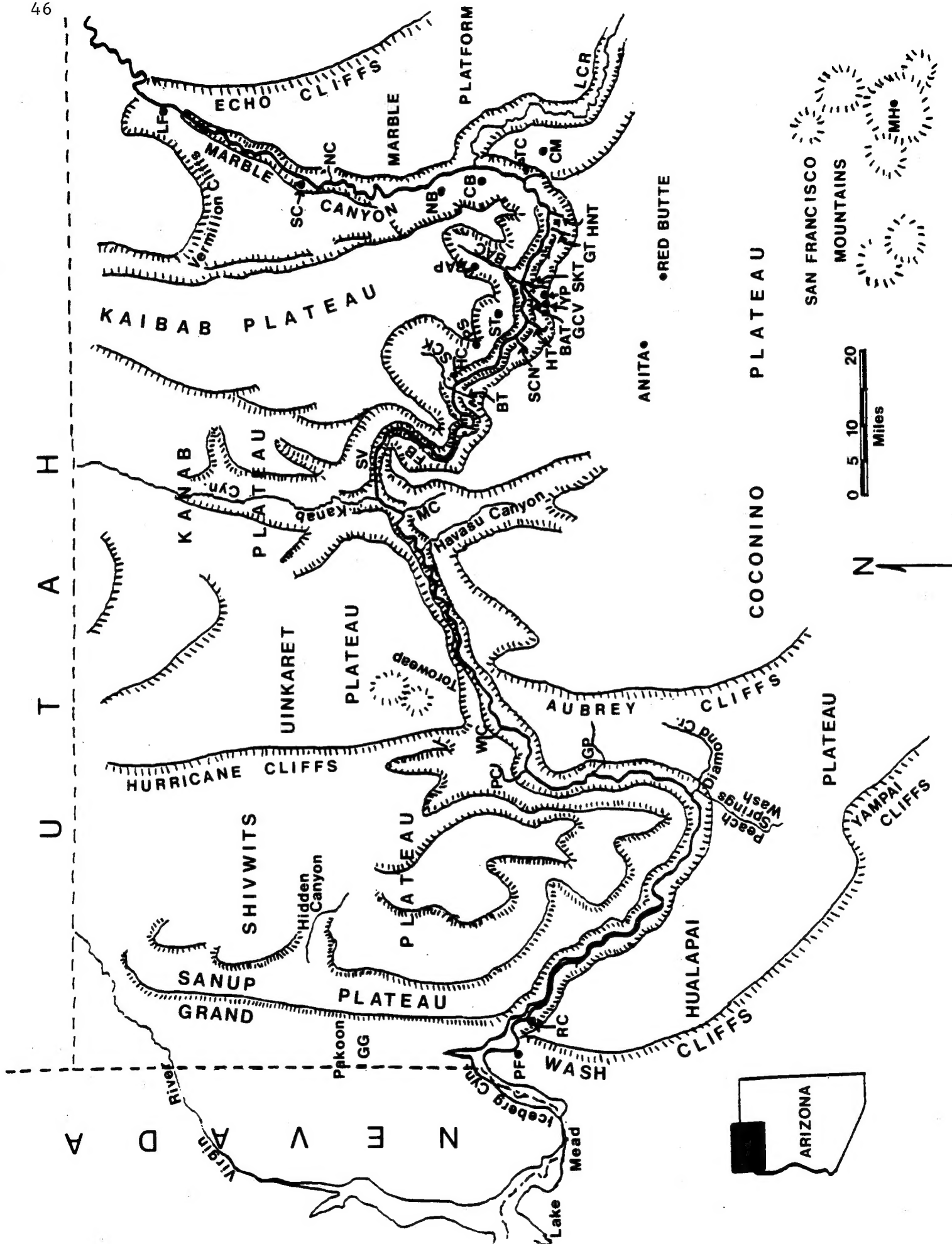
Introduction

"The sea must have been here once."

Edwin D. McKee, who figures at the forefront of contemporary Grand Canyon geology, began his long association with the Canyon as Park Naturalist at Grand Canyon National Park during the late 1920s and 1930s. He tells the story (McKee, 1948) of the day he had been working at an outcrop on the South Rim, examining a well-preserved fossil shell, when an elderly couple happened by. The man's curiosity piqued, he stopped to see what McKee was doing. After some thought, he turned to his wife and remarked, "The sea must have been here once."

That is what the geological method is all about--observation and interpretation. Few places on earth offer a field for research as geologically and aesthetically overwhelming as does the Grand Canyon. Our powers of observation and interpretation are well exercised there. The story of life recorded in the Canyon's rocks is well-told and remarkably complete for a single locality..

The Grand Canyon of the Colorado River extends more than 200 miles east to west across northwestern Arizona (Fig. 1); in its eastern portion it is more than a mile deep and about 12 miles wide. Rocks ranging from Precambrian to Early Triassic age comprise the stratigraphic sequence (Table 1; Figs. 2, 3). The base of this column is occupied by a 1.7-billion-year-old crystalline basement complex (the Vishnu Complex and related rocks) and a late Precambrian wedge of sedimentary



and igneous rocks (the Grand Canyon Supergroup). Overlying them is a thick sequence of Paleozoic strata. But several major unconformities interrupt this grand stratigraphic pile: 1) the unconformity at the top of the metamorphic basement complex, representing a stratigraphic hiatus of at least 300 million years; 2) a major(?) unconformity within the Grand Canyon Supergroup, perhaps as long as 300 m.y.; 3) the "Great Unconformity," an angular unconformity separating the Precambrian and Paleozoic strata, about 300 m.y.; 4) the unconformity at the top of the Tonto Group, separating the Middle Cambrian and the Late Devonian strata, about 150 m.y. Other, shorter-term unconformities occur throughout the section. Mesozoic rocks, unconformably overlying the Permian Kaibab Limestone, are eroded from all but a few scattered localities at or near the Canyon rim, although within sight of the Canyon there are great cliffs of these strata.

Fossils are found in nearly all of the Grand Canyon's formations, and the diversity of these fossils is great. Late Precambrian micro- and macroscopic fossils continue to stimulate invigorating discussions on their biologic and paleoecologic significance. Invertebrate faunal zones in the Paleozoic rocks can be traced great distances through the Canyon. From this paleontological evidence some basic theorems of stratigraphy have evolved. The recent discovery of buried Chesterian (Late Mississippian) valleys, dated paleontologically, has written a new page in the Grand Canyon story. Footprints and trackways of invertebrates and vertebrates occur in Pennsylvanian and Permian red beds and Permian desert dunes. The red beds also contain a unique Early Permian flora. Paleozoic vertebrate remains, although scant, include a rare and problematical genus of Permian shark, first discovered in the Grand Canyon. Late Cenozoic fossils occur within and near the Canyon; and the late Pleistocene-Holocene cave deposits of the Canyon have provided detailed evidence of the interrelationships of plants, animals, and climates

during the advance and retreat of the great continental ice sheets. And, for the "pseudopaleontologist," the Grand Canyon includes some fine examples of those paleontological false alarms, pseudofossils.

The well-documented lithologic and biotic record of the Grand Canyon is due to a number of fortuitous geologic circumstances: astoundingly unobscured exposures in a mostly semiarid environment, well-defined key beds, classic depositional cycles, the preservation of widely different sediment types through a very long period of geologic time, and only slight structural disturbance of nearly horizontal strata. We cannot realistically expect a more instructive lesson in geology and paleontology, in one locality, than that proffered by the Grand Canyon.

Biostratigraphic, paleoecologic, and taxonomic works fill the Grand Canyon literature, but no single review of all of Grand Canyon paleontology has been published. It falls upon this paper to collate 125 years of abundant investigations at this grand outcrop--investigations by many scientists, among whom are some of the most renowned researchers of the 19th and 20th centuries. So much has been learned from the Grand Canyon strata that, for the sake of brevity, this paper is an historical survey rather than a comprehensive synthesis of biostratigraphy and paleoecology. Such a synthesis would require monographic treatment encompassing a much broader geographic range than that addressed by this paper. Biostratigraphic and paleoecologic surveys can be found among the works cited herein. This paper, as an historical review, also illuminates the roles the fossils and their investigators have played in interpreting the region's geologic history, pointing out the contributions they have made to the development of geologic principles.

The Grand Canyon's pageant of life extends from the early scenes of life on earth, in the late Precambrian sediments, to the present. Its interpretation is constantly undergoing revision,

Figure 1. The Grand Canyon of the Colorado River--Geographic Features of the Grand Canyon Area, Including Sites Mentioned in the Text.

ABBREVIATIONS:

| | | | | | |
|-----|------------------------------|-----|--|-----|--------------------|
| BAC | Bright Angel Canyon | HC | Hotauta Canyon | PS | Point Sublime |
| BAP | Bright Angel Point | HNT | Hance Trail | RC | Rampart Cave |
| BAT | Bright Angel Trail | HT | Hermit Trail | SC | Stanton's Cave |
| BT | Bass Trail | LCR | Little Colorado River | SCK | Shinumo Creek |
| CB | Carbon Butte | LF | Lees Ferry | SCN | Sapphire Canyon |
| CM | Cedar Mountain | MC | Matkatamiba Canyon | SKT | South Kaibab Trail |
| FB | Fossil Bay and Fossil Canyon | MH | Mount Humphrey (highest point in Arizona, 12,633 ft) | ST | Shiva Temple |
| GCV | Grand Canyon Village | NB | Nankoweap Butte | SV | Surprise Valley |
| GG | Grand Gulch | NC | Nautiloid Canyon | TC | Tanner Canyon |
| GP | Granite Park | PC | Parashant Canyon | WC | Whitmore Canyon |
| GT | Grandview Trail | PF | Pierce's Ferry | YP | Yavapai Point |

and to this end I include in this paper a few new remarks on the Grand Canyon paleobiota, some by me but most by kind and interested correspondents. But modern life, too, is constantly revised--by evolution. A section of this paper is devoted to the continuing processes of evolution as observed at the Grand Canyon today.

From all of this--the human history, the history of life on earth, the diversity of taxa--the reader will hopefully gain a deeper appreciation for the amazing story told by the Grand Canyon. Perhaps a few industrious researchers will also be inspired to pursue some of the areas of needed investigation.

125 Years of Research

Although Europeans were first led to the Grand Canyon by native inhabitants in 1540, purposeful attempts to explore it did not take place for more than 300 years. Sitgreaves (1853) recorded in his journal two aborted attempts to reach the Canyon during his 1851 reconnaissance of the areas east and south of the Grand Canyon. Hitchcock's (1857) paper on erosional landforms includes a brief mention of "Big Cañon" (as it was then known) but he was unable to find a "detailed account of its extent." Relying on Sitgreaves' description of the gorge of the Little Colorado River near Grand Falls, where its depth is 120 feet, Hitchcock (1857, p. 116) suspected that this depth was "less probably than that of the Big cañon." He further indicated (p. 125) that the canyons of the Southwest are "Very old." This constitutes the first mention of the Grand Canyon in a scientific perspective--to my knowledge this has never been noted in the literature.

The honor of the first exploration of the Grand Canyon went to Joseph C. Ives' lower Colorado River exploring expedition. Ascending the Colorado in a specially built steamer as far as Black Canyon, just downstream from present-day Hoover Dam, the Ives party then trekked overland and reached the western part of Big Cañon, near Diamond Creek, on April 3, 1858. The geologist attached to the expedition, John Strong Newberry, is the acknowledged pioneer of Grand Canyon geology, and his "Geological Report" (Newberry, 1861) includes the first descriptions of Grand Canyon fossils. Although some early publications have indicated that Newberry's collections were deposited with Columbia University (*e.g.*, Jackson, 1912, pp. 261, 267-268), they are in fact in the U.S. National Museum (F. J. Collier, written commun., 1982).

John Wesley Powell, the patriarch of Colorado River exploration and western development, in 1869 led the inaugural river run through what he named the Grand Canyon. His final report (Powell, 1875) interweaves observations and events from his 1869 and 1871-1872 expeditions as though a single journey, but it remains the classic chronicle of the opening of the Grand Canyon. Powell does not allude to paleontological discoveries in

this report. Instead, his first mention of Grand Canyon fossils is in his geological monograph on the Uinta Mountains of Utah (Powell, 1876). C. A. White's (1876) report on Uinta paleontology also mentions these fossils.

By the time Powell got around to publishing his narrative, the whole Colorado Plateau had become widely known as one of the greatest geological lessons in the world. Gilbert (1876, p. 103) wrote of this:

"Already the field has yielded to its students results which are new to them, and which are probably new to the world of science. Among them are a type of uplifted mountains, a type of eruptive mountains, a theory of waterfalls, and a classification of drainage systems."

If in so short a time so many major contributions to science could be made from studying one region, it is no wonder that geologists began to show great interest in the Colorado Plateau.

The first in-depth paleontological work in the Grand Canyon was conducted by Charles D. Walcott in the summer of 1879. Traveling down tortuous Kanab Canyon, a tributary to the Colorado River in central Grand Canyon, Walcott made the first extensive collection of Grand Canyon fossils and published the first study of the Paleozoic strata there (Walcott, 1880). (For a geological travelogue of this "Trail of Scientists," see McKee, 1946.) In later years, through the beginning of the 20th century, Walcott returned to the Grand Canyon several times, where he added to his worldwide researches on late Precambrian and Cambrian paleontology and paleogeography. At least 30 of his subsequent publications, from 1883 to 1925, deal in whole or in part with the Grand Canyon and its fossils (*cf.* Spamer, 1983). (See Pyne, 1982, pp. 27-28, for an historical overview of some of Walcott's Grand Canyon work. Refer to this reference and to Spamer, 1983, for other discussions of geological studies in the Grand Canyon.)

Early work by Gilbert (1875), Marvine (1875), Powell (1876), Walcott (1880, 1883, 1886a,b, 1890a,b, 1891a,b, 1894, 1895) and Dutton (1882) laid the stratigraphic groundwork into which existing and subsequent fossil collections would fit. The concepts of biostratigraphy were not well defined at that time, and faunal assemblages were useful to correlation only in the most general of aspects. Beginning at the turn of the century, more refined stratigraphic studies were made in the Grand Canyon country. The critical results were reported by Ransome (1908, 1917), Darton (1910, 1925), Schuchert (1918a,b), Reeside & Bassler (1922), Moore (1925), Longwell (1921, 1928, 1936), and Stoyanow (1936). Surveys of fossils in these early works were not so much concerned with correlations within the Grand Canyon region as they were with other units beyond the area. The faunal lists were, however, valuable to later researchers who recognized the

| Supai Group | | Permian | | Pennsylvanian | | Mississippian | | Devonian | | Devonian or Late or Middle Cambrian | |
|------------------------|------------------|---|--|--|--|--|--|------------------|--|-------------------------------------|--|
| | | Early | | | | | | Late | | | |
| | | Wolfcampian | | Virgilian | | Chesterian | | Frasnian | | Givetian | |
| | | indet. boundary | | Des Moinesian (?) | | Morrowan | | Famennian | | Mdl. | |
| | | Four Transgressive-Regressive Cycles | | | | | | | | | |
| Esplanade | Pakoon Limestone | Sandstones, sandy mudstones Pakoon: Limestones | | Convergence of two transgressing seaways(?) Pakoon: Barrier buildup | | Erosion of uplifted area; fluvio-marine infilling of valleys | | Intertidal shelf | | Shallow supratidal shelf | |
| Sandstone | | 250-800 | | Basal conglomerate | | Limestones, bedded cherts | | 0-1,000 | | Dolomites | |
| Wescogame Formation | | 100-250 | | Sandstones, sandy mudstones Basal conglomerate | | Dolomites and limestones | | 500 | | | |
| Manakacha Formation | | 200-300 | | Sandstones, sandy mudstones, limestones | | Bedded cherts and dolomites | | 70-100 | | | |
| Watahomigi Formation | | 100-350 | | Mudstones, sandy mudstones, limestones; intraformational conglomerates Basal conglomerate | | Fine-grained dolomites | | 100 | | | |
| unassigned | | 0-400 | | Marine and continental sediments filling buried valleys in western Grand Canyon | | Eastern Grand Canyon: Discontinuous carbonate channel-fill deposits in top of Muav ls. Western Grand Canyon: Carbonate channel fill overlain by dolomites | | 0-1,000 | | | |
| Redwall Limestone | Horseshoe Mesa | 35-125 | | Limestones, bedded cherts | | Dolomites and limestones | | 500 | | | |
| | Mooney Falls | 200-350 | | Dolomites and limestones | | Bedded cherts and dolomites | | 70-100 | | | |
| | Thunder Springs | 70-100 | | Bedded cherts and dolomites | | Fine-grained dolomites | | 100 | | | |
| | Whitmore Wash | 100 | | Fine-grained dolomites | | Eastern Grand Canyon: Discontinuous carbonate channel-fill deposits in top of Muav ls. Western Grand Canyon: Carbonate channel fill overlain by dolomites | | 0-1,000 | | | |
| Temple Butte Limestone | | 0-1,000 | | Eastern Grand Canyon: Discontinuous carbonate channel-fill deposits in top of Muav ls. Western Grand Canyon: Carbonate channel fill overlain by dolomites | | Dolomites | | 70-150 | | | |
| unassigned | | 70-150 | | Dolomites | | | | | | | |

| Paleozoic | | Cambrian | | | | | |
|-------------|--------------------|------------------------|---------|---|--|---------------------------------------|--|
| | | Middle | | | | Early | |
| Tonto Group | Muav Limestone | Havas | | | Limestones | Regressing sea | |
| | | Gateway Canyon | | | Limestones, siltstones | Maximum advance, beginning regression | |
| | | Kanab Canyon | | Mottled | Limestones, siltstones, shales, dolostones, sandstones | Transgressing sea | |
| | | Peach Springs | | grey | Limestones | Transgressing sea | |
| | | unnamed unit | 150-800 | | Shales | Regressing sea | |
| | | Spencer Canyon | | lime- | Limestones, siltstones | Transgressing sea | |
| | | unnamed unit | | stones | Shales | Regressing sea | |
| | | Sanup Plateau | | | Limestones, siltstones | Transgressing sea | |
| | | unnamed unit | | | Shales | Regressing sea | |
| | | Rampart Cave | | | Limestones, shales | Transgressing sea | |
| | Bright Angel Shale | Flour Sack | | Shaly | Shales, siltstones, limestones | Regressing sea (minor) | |
| | | Meriwitica | | mud- | Dolomites | Transgressing sea | |
| | | unnamed unit | | stones, | Shales | Regressing sea | |
| | | Tincanabits | 200-450 | sand- | Dolomites | Transgressing sea | |
| | | unnamed unit | | stones, | Shales | | |
| | | red-brown sandstone | | silt- | Sandstones | | |
| | | unnamed unit | | stones | Shales | | |
| | | transition zone | 100-300 | Coarse- to medium-grained cross-bedded sandstones | | Offshore | |
| | | Tapeats Sandstone | | | | Shoreline | |
| | | The Great Unconformity | | | | | |

Precambrian Y

| Grand Canyon Supergroup | | | | Chuar Group | |
|-------------------------|---|-------|---|--|--|
| Sixtymile Formation | Lower, middle, and upper; unconformable | 120 | Lower, middle, and upper; unconformable | The Great Unconformity | |
| Kwagunt Formation | Walcott | 838 | 2,218 | Contemporary landslide debris | |
| | Awatubi | 1,128 | | { Contemporary earthquake shock or sea-floor slumping | |
| | Carbon Butte | 252 | | | |
| Galeros Formation | Duppa | 570 | | Primarily shallow-water deposits, with some evidence of subaerial exposure | |
| | Carbon Canyon | 1,546 | | | |
| | Jupiter | 1,516 | 4,272 | | |
| | Tanner | 640 | | | |
| Nankoweap Formation | upper member, ferruginous member | 330 | | Nearshore to marginal marine | |

| Grand Canyon Supergroup | | Precambrian Y | | Precambrian X | |
|-------------------------------|----------------------|---------------|---|---|--|
| Cardenas Lavas | | 980 | Lavas, interbedded sands | Shallow-water and subaerial eruptions | |
| Dox Formation | Ochoa Point | 304 | Sandstones, siltstones | Tidal flats | |
| | Comanche Point | 623 | Interbedded siltstones, quartz sandstones | Tidal flats, salt flats | |
| | Solomon Temple | 3,145 | Sandstones, fine-grained sandstones, shaly siltstones | Upper: Channeled floodplain Lower: Floodplain | |
| | Escalante Creek | 1,291 | Siltstones, sandstones, calcareous sandstones, shales | Deltaic, turbidite, with basal lagoonal shale | |
| Shinumo Quartzite | 5 units | 1,132-1,346 | Dominantly sandstones, conglomerates | Fluvio-deltaic | |
| Hakatai Shale | 4 units | 558-949 | Mudstones, sandstones, intruded by sills | Shallow-water, subaerial exposure in arid climate | |
| Bass Limestone | Hotauta Conglomerate | 187-327 | <i>gradational contact</i> Dolomites, cherts, shales, mudstones, intermittent basal conglomerate | Transgression-regression in embayment(?) | |
| Vishnu Complex (primary unit) | | | | | |
| Zoroaster Plutonic Complex | | | | | |
| Trinity Gneiss | | | | | |
| Elves Chasm Gneiss | | | | | |
| Granite Park Mafic Complex | | | | | |
| | | Basement | Metamorphosed sands, shales, and igneous rocks, including plutons and pegmatites | | |

Notes:

1. This table has been compiled from many sources. Most figures of thicknesses and lithologic descriptions are generalized.
2. Some formations and stratigraphic members are not continuous through the length of the Grand Canyon. The Pakoon Limestone is not a part of the Supai Group.
3. Unnamed members within the Muav Limestone and Bright Angel Shale adopted from Billingsley (1978).
4. The "Great Unconformity" is an angular unconformity. Rocks of the Grand Canyon Supergroup are exposed only in the eastern Grand Canyon.
5. Rocks of the Vishnu Complex and related rocks form the Grand Canyon's Inner Gorge, most dramatically developed in the eastern section where >1,100 vertical feet are exposed.

stratigraphic significance of facies and key faunal beds. During this period, too, these workers gathered enough expertise to depart from the generalized interpretations of Gilbert, Marvine, Powell, Dutton, and Walcott; their work contributed to a healthy dialogue of geological observation, interpretation, and opinion.

The 1920s also opened two new areas of investigation in the Grand Canyon: the remarkable ichnofauna and flora of the Supai Group and Hermit Shale. Charles W. Gilmore, working for the U.S. National Museum and the National Park Service, with the support of the National Academy of Sciences, undertook the only exhaustive study of the Grand Canyon late Paleozoic ichnofauna. David White, with the support of the Carnegie Institution of Washington, made the only complete study of the unique Early Permian flora.




























Beginning in the 1930s, information on the Grand Canyon Paleozoic strata and fossils burgeoned. These researches revolve about the work and techniques of Edwin D. McKee. He developed in the Grand Canyon some of the basic stratigraphic principles, including the concepts of litho- and biofacies and the principle of tracing key beds as indicators of correlation and tools of time-rock stratigraphy. These principles were first employed by McKee (1938b) in his monograph on the Kaibab Limestone and Toroweap Formation. They were refined further in his subsequent monographs on the Cambrian Tonto Group (McKee & Resser, 1945), the Mississippian Redwall Limestone (McKee & Gutschick, 1969), and the Permian-Pennsylvanian Supai Group (McKee, 1982).

Figure 2. Generalized Stratigraphic Column of the Grand Canyon Showing Lithology, Topographic Expression, Characteristic Paleobiota, and Ranges of Late Pleistocene-Holocene Floral Assemblages.

Notes:

1. Relative average thicknesses of rock formations are to scale. Not all stratigraphic members are continuous through the length of the Grand Canyon, nor are formational thicknesses constant.
2. Illustrations of topographic expression are limited mostly to cliff- and slope-forming characteristics. Note that lithostratigraphic boundaries do not always coincide with changes in topographic expression. Position of Rampart Cave is stratigraphically approximate; topographically, the cave is 500 ft above the Colorado River in westernmost Grand Canyon where the basal Tonto Group and Precambrian rocks are not exposed.
3. Characteristic paleobiota shown do not imply relative abundances. Horizontal divisions delineate formational boundaries.
4. Distributions of late Cenozoic flora do not necessarily correlate with lithostratigraphic divisions; only generalized distributions and floral content are implied, as represented in eastern Grand Canyon.

SYMBOLS

| Lithology | | Paleobiota | | | |
|---|--------------|---|------------------|---|---|
|  | limestone |  | brachiopods |  | corals |
|  | dolomite |  | molluscs |  | bryozoans |
|  | shale |  | trilobites |  | crinoids |
|  | siltstone |  | cephalopods |  | echinoids |
|  | sandstone |  | other gastropods |  | insects |
|  | cherts |  | foraminifera |  | stromatolites |
|  | conglomerate |  | conodonts |  | algae |
|  | metamorphic |  | fish |  | ichnites |
|  | pegmatite |  | plants |  | trace fossils other than ichnites |
| | lavas | | | | |

Late Cenozoic



spruce forest



fir or limber pine forest



juniper and affiliated taxa

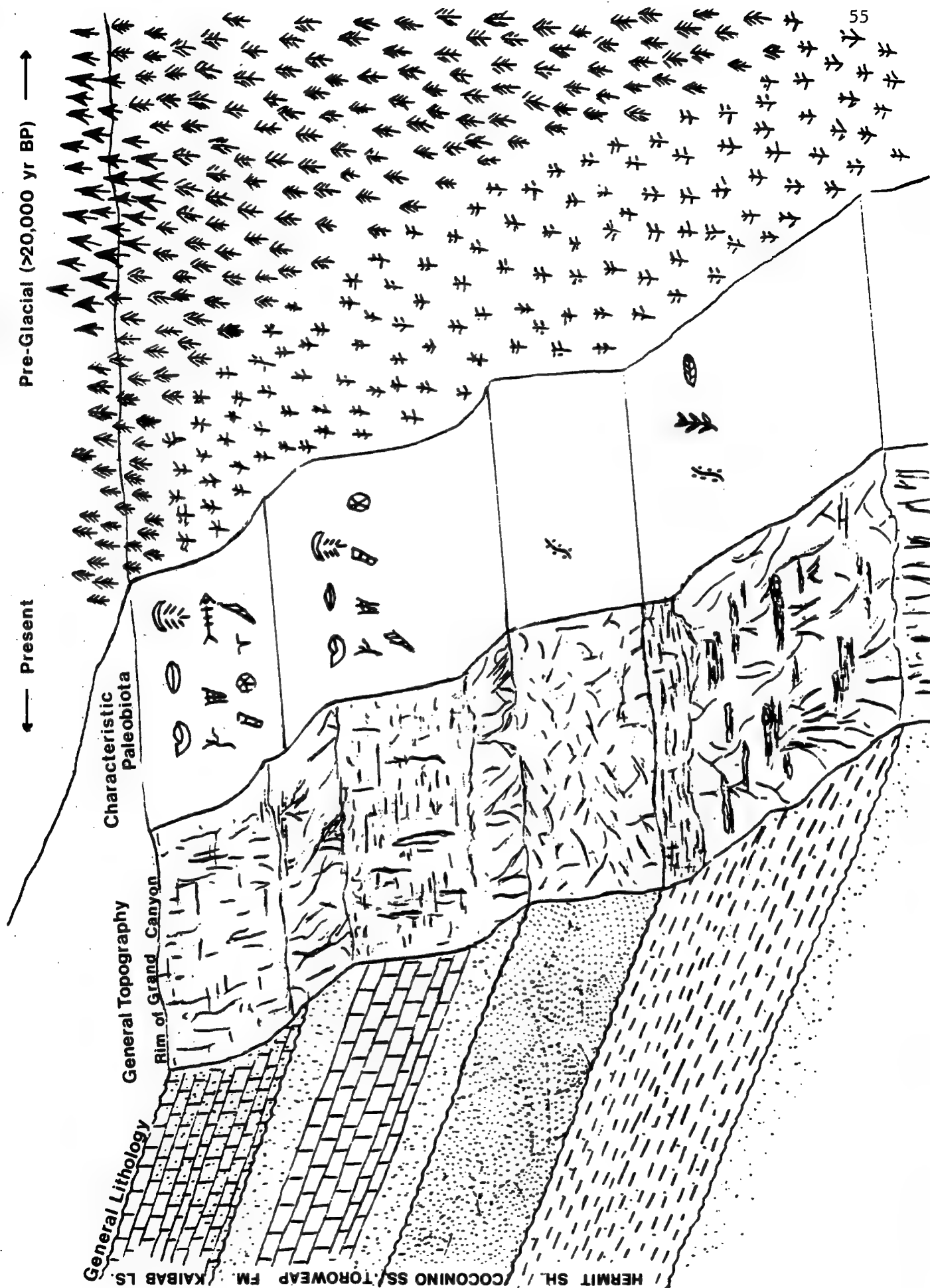


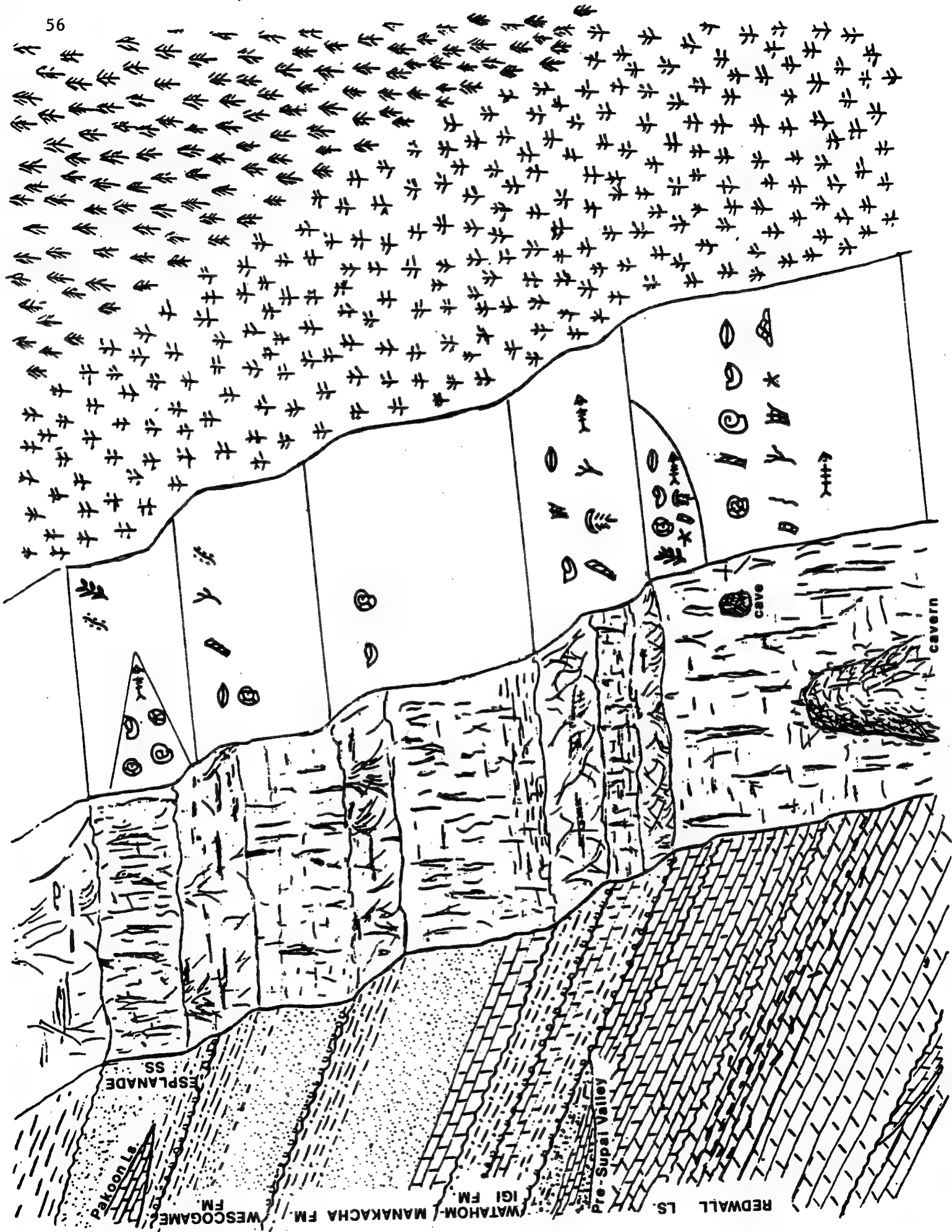
desert scrub

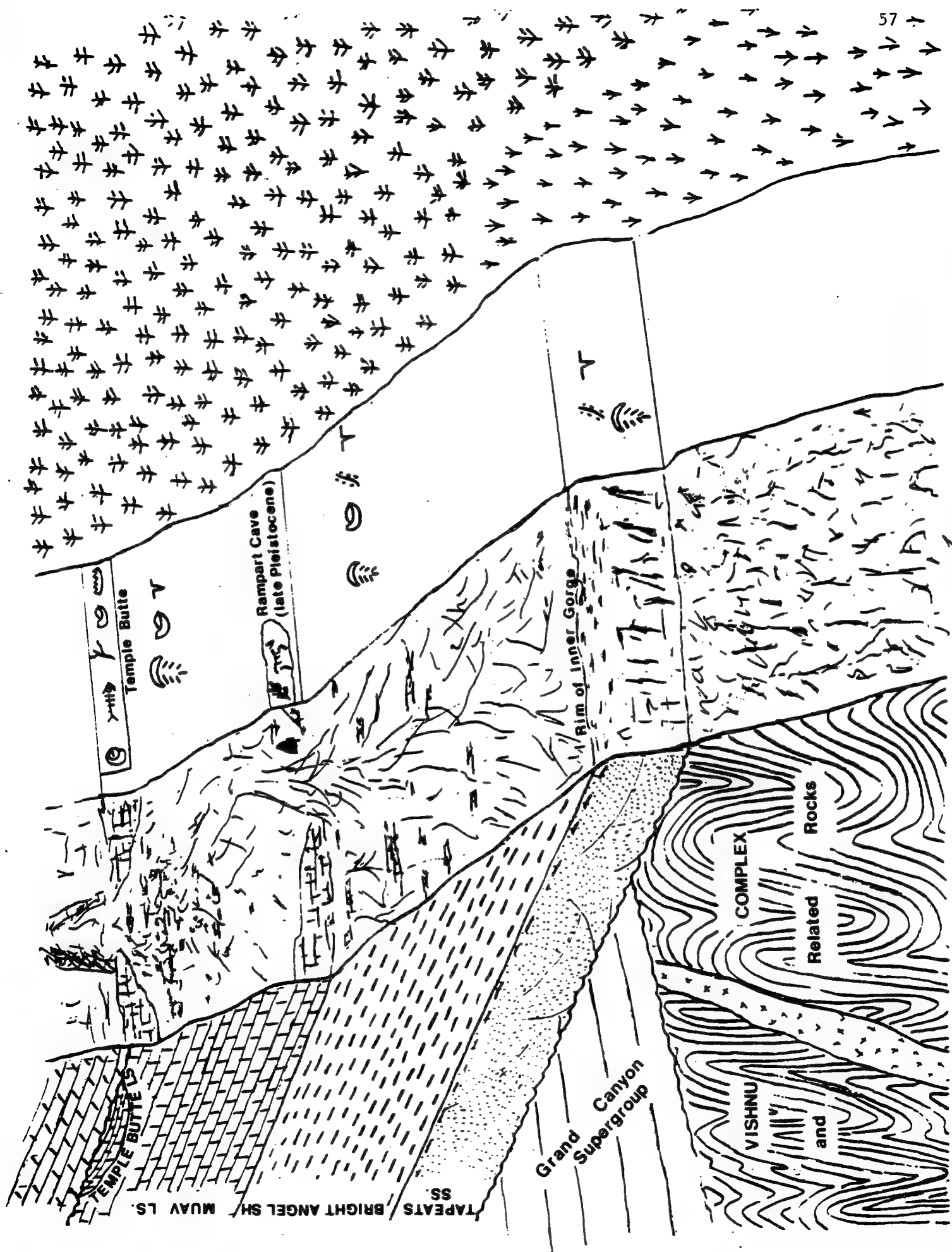
LATE CENOZOIC ENVIRONMENTS

Present

Pre-Glacial (>20,000 yr BP) →







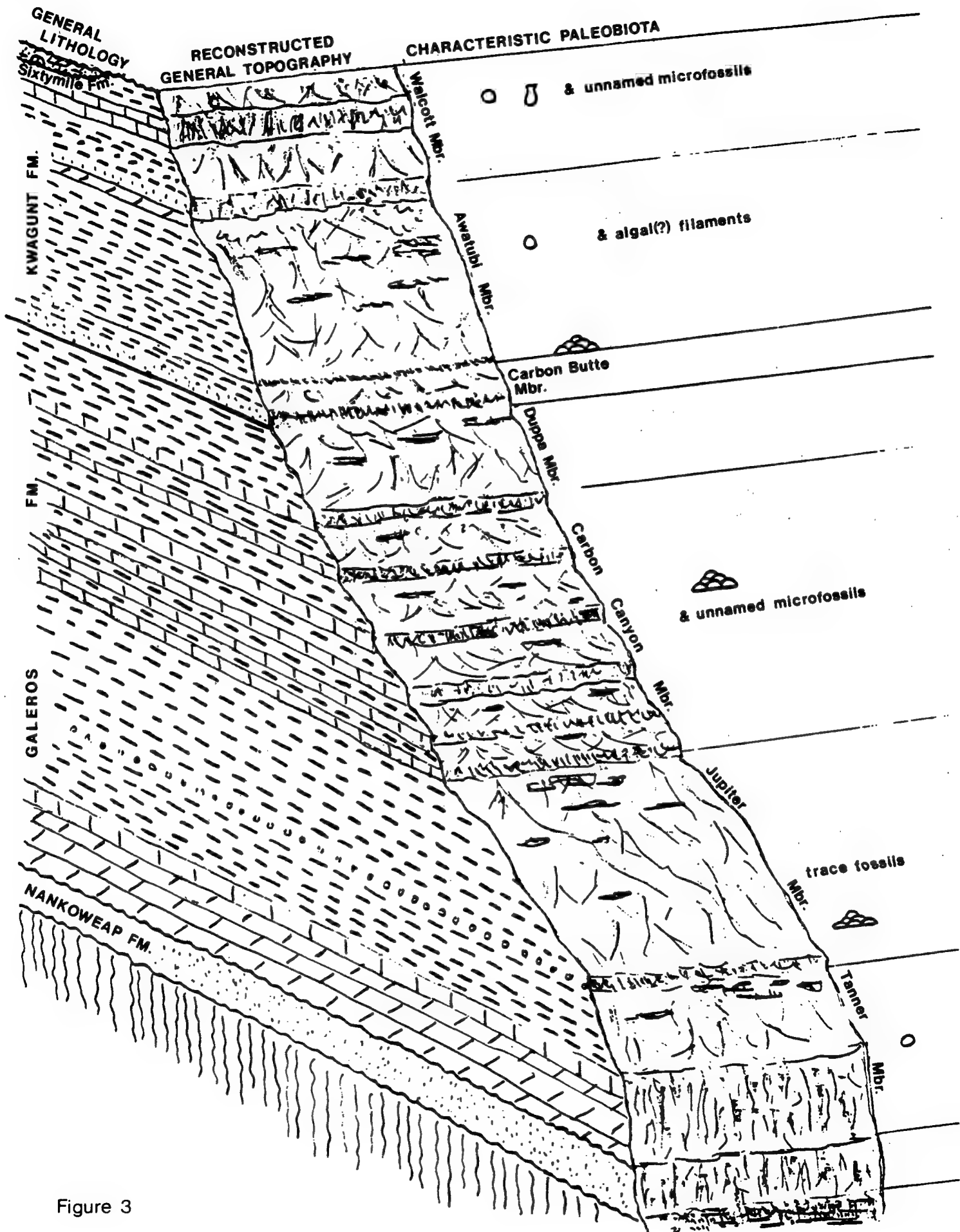


Figure 3

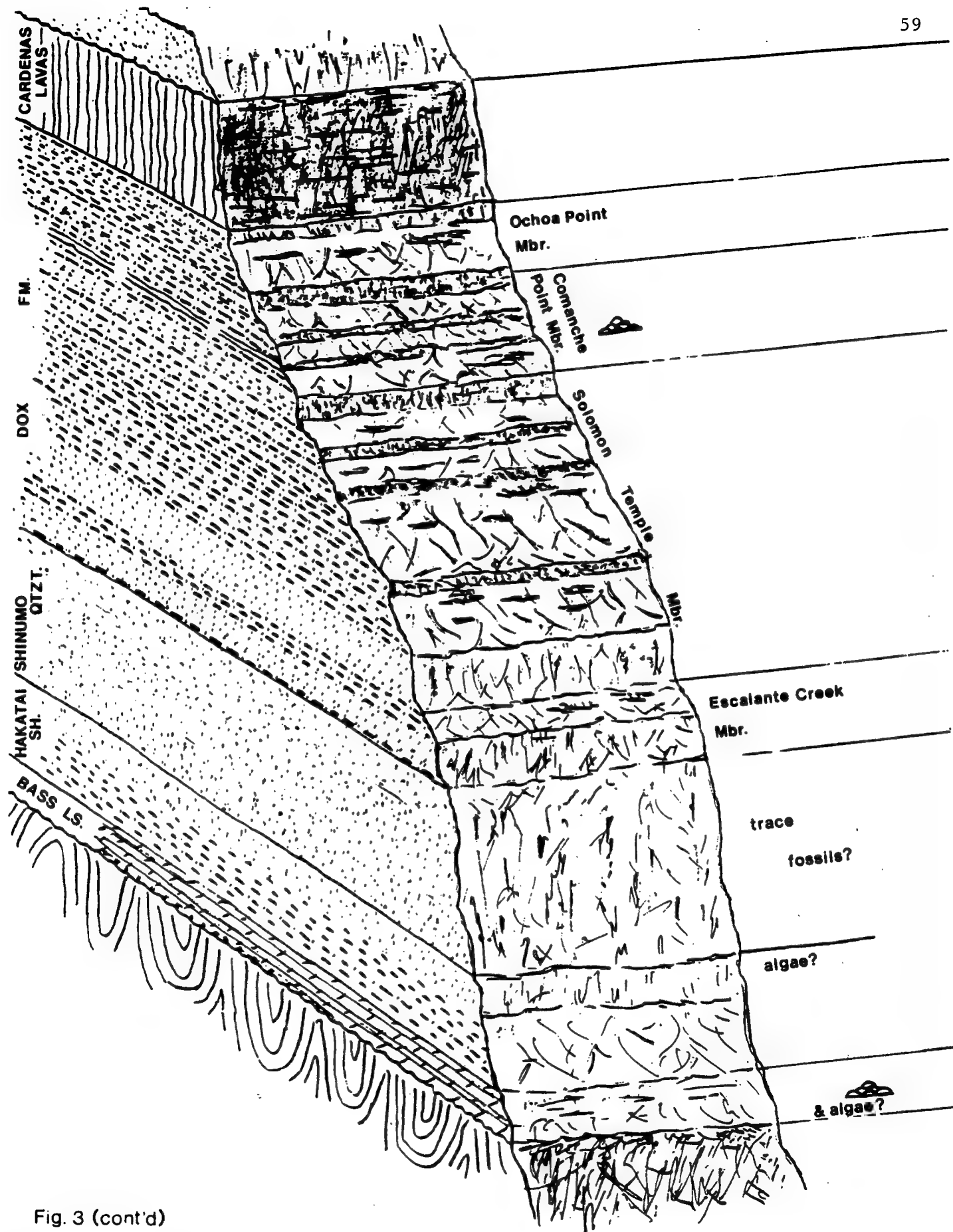


Fig. 3 (cont'd)

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Between the 1930s and 1960s, publications that in whole or in part dealt with the Grand Canyon were restricted primarily to problems in paleogeography, paleotectonics, stratigraphic correlation and age, and sedimentology. Paleontological studies were few, with the notable exceptions of monographs by McKee (1938b) and McKee & Resser (1945). Many miscellaneous paleontological works, however, included new fossils or had applications to existing groups from the Grand Canyon; they are cited throughout this paper.

Since the 1960s, Grand Canyon geological research has experienced a renaissance. Much of this new work was instigated by the centenary of the Powell expeditions. The late Precambrian Grand Canyon Supergroup for the first time came under micropaleontological scrutiny. Microfossils were first recognized in the Chuar Group, and the alleged Chuar macrofossils described by Walcott in the late 1800s were finally, formally, banished to the realm of pseudofossils. With this revived interest in the stratigraphy of the Grand Canyon region, and in the significance of its paleofauna, we are beginning to see some new interpretations of the stories read from the rocks. This paper hopefully places in perspective the history behind our current paleontological knowledge of the Grand Canyon.

In looking back over 125 years of paleontological studies in the Grand Canyon, we would be surprised if no new species of fossils had been found. The literature records the names of many taxa that were first described from the Grand Canyon or from nearby--the list of currently valid taxa includes 180 species in 107 genera, of which 30 were new genera (Table 2). No new suprageneric groups have been founded on Grand Canyon type fossils. Of course, this list is always subject to revision as new taxonomic names are introduced and reassignments are made. Table 3 lists the Grand Canyon type fossils that have been declared to be synonyms of other species; more are suspected by some researchers to be misidentified or wholly invalid. Although some Grand Canyon type

species and genera may succumb to taxonomic reassignment, the names remain on record as contributions to the interpretation of Grand Canyon strata.

The Grand Canyon types came from throughout the stratigraphic sequence and include protist, invertebrate, vertebrate, plant, trace, and problematical taxa, as well as two "species" of what later were demoted to the ranks of pseudofossils. For a catalogue of the Grand Canyon type fossils, see Spamer (1983, 1984). A table comparable to Table 2 for all Grand Canyon fossils cannot be compiled at this time; there are some important collections still in study that would make any such compilation unworthwhile and certainly inaccurate.

Late Precambrian Fossils

The thick sequence of late Precambrian sediments in the eastern Grand Canyon--the Grand Canyon Supergroup--has yielded a number of interesting fossils. The first of these fossils were described in passing by Powell (1876), who remarked that little could be made of them. White (1876) elaborated on these fossils, considering some of the forms to be brachiopods. In 1883, Walcott reported what we now know are stromatolites from these rocks; he called them "an obscure Stromatopora-like group of forms" (Walcott, 1883, p. 441) and "concretionary limestones" (Walcott, 1894, pp. 508 ff.). Some fossils initially led Walcott astray, leading him to assign these rocks a Cambrian age (Walcott, 1883, 1884). He later (1886b) revised this assignment, placing the Grand Canyon Supergroup in the Precambrian. While many later workers cited Walcott's publications, systematic treatment of the Supergroup fossils was not undertaken until the 1960s. Microscopic examination of some of the strata of the Supergroup have revealed complex interrelated groups of microfossils. Walcott's Precambrian megafossils are now recognized to be pseudofossils and have been formally abandoned.

Figure 3. Generalized Stratigraphic Column of the Late Precambrian Grand Canyon Supergroup Showing Lithology, Reconstructed Topographic Expression, and Characteristic Paleobiota.

Notes:

1. Relative average thickness of rock formations are to scale (but at a smaller scale than those in Fig. 2). The Grand Canyon Supergroup is a block-faulted sequence of strata dipping 15° to the northeast, exposed discontinuously through eastern Grand Canyon. The stratigraphic column here is a reconstructed sequence. Refer to Fig. 2 for explanations of lithologic symbols.
2. The general topographic expression illustrates the relative resistance to erosion of various strata in a reconstructed horizontal stratigraphic column.
3. Characteristic paleobiota shown do not imply relative abundances. Horizontal divisions delineate boundaries between stratigraphic formations and members.

Paleobiological Symbols:



Chuaria



Melanocyrrillum



stromatolites

Table 2. Summary of Grand Canyon Type Fossils¹

| Group | Total Genera | No. of Type Genera | No. of Type Species | No. of Type Sub- species |
|--------------------------------|-----------------|--------------------------|---------------------------|--------------------------------|
| Invertebrates | | | | |
| Foraminifera | 6 | -- ² | 8 | 2 |
| Bryozoans | 4 | 1 | 4 | |
| Coelenterates | 2 | | 2 | |
| Brachiopods | 14 | 1 | 24 | 1 |
| Monoplacophors | 1 | | 1 | |
| Cephalapods | 1 | | 2 | |
| Ammonoids | 1 | | 1 | |
| Trilobitoids | 1 | 1 | 1 | |
| Trilobites | 22 | 2 | 38 | |
| Ostracodes | 4 | 1 | 22 | 1 |
| Insects | 1 | | 2 | |
| Blastoids | 1 | | 1 | |
| Eocrinoids | 1 | | 1 | |
| Echinoids | 1 | | 3 | |
| Total Invertebrates | 60 | 6 ³ | 110 | 4 |
| Vertebrates | | | | |
| Chondrichthyans | 1 | 1 | 1 | |
| Mammals ⁴ | 6 | 1 | 6 | |
| Total Vertebrates | 7 | 2 | 7 | |
| Trace Fossils | | | | |
| Invertebrates | 8 | 6 | 9 | |
| Vertebrates | 14 | 10 | 23 | |
| Total Trace Fossils | 22 | 16 | 32 | |
| Plants | | | | |
| Arthropytes | 1 | | 1 | |
| Pteridosperms | 5 | 2 | 14 | |
| Conifers | 5 | 1 | 7 | |
| Fruits of Uncertain Affinities | 2 | 1 | 2 | |
| Total Plants | 13 | 4 | 24 | |
| Miscellanea | | | | |
| Stromatolites | 1 | | 1 | |
| Problematica | 2 | 2 | 4 | |
| Pseudofossils | 2 | | 2 | |
| Total Miscellanea | 5 | 2 | 7 | |
| GRAND TOTAL | 107 | 30 ³ | 180 | 4 |

¹Includes revisions as listed in Table 4. (From Spamer, 1984, p. 69.)²One new subgenus³Plus one subgenus⁴From Anita, Arizona (see text)

Table 3. Grand Canyon Type Fossils: Names Declared Synonymous with Other Taxa¹

| Current Status ² | Grand Canyon Type Fossil No. ³ | Junior Synonym ² | Grand Canyon Type Fossil No. ³ | Reference |
|---|--|---|--|--------------------------------|
| Vertebrates | | | | |
| <i>Hemiauchenia blancoensis</i> (Meade), 1945 | -- ⁴ | <i>Procamelus longurio</i> Hay, 1921 ^{5,6} | 111 | Webb (1974) |
| <i>Taxidea tarus</i> (Schreber), 1778 | -- ⁴ | <i>Taxidea robusta</i> Hay, 1921 ⁵ | 116 | cf. Kurtén & Anderson (1980) |
| Ichnites of Vertebrates | | | | |
| <i>Baropezia eakini</i> Gilmore, 1926 | 131 | <i>Baropus coconinoensis</i> Gilmore, 1927 | 132 | Baird (1952) |
| <i>Barypodus metzgeri</i> Gilmore, 1927 | 134 | <i>Nanopus marinus</i> Gilmore, 1927 | 146 | cf. Baird (this paper) |
| <i>Batrachichnus delicatulus</i> (Lull), 1918 | 136 | <i>Dromillopus parvus</i> Gilmore, 1927 | 140 | Baird, cf. Breed (1967) |
| <i>Tridentichnus supaiensis</i> Gilmore, 1927 | 151 | <i>Ammobatrachus turbatus</i> Gilmore, 1928 | 129 | Baird in Lewis & Vaughn (1965) |

¹ Including written communications cited by Breed (1967) and this paper.² Gilmore (1926, 1927, 1928), = Gilmore, 1926b, 1927b, 1928b of references cited in this paper.³ Cf. Spamer (1983, 1984); junior synonyms retain Type Fossil Numbers as a matter of historical record.⁴ *H. blancoensis* and *T. tarus* are not Grand Canyon type fossils.⁵ From Anita, Arizona; see text.⁶ Webb (1974, pp. 200-201) declared that "*P. longurio*" Hay, 1921, is "an inadequate type specimen"; as such, the specific name does not have priority over *H. blancoensis* (Meade), 1945.

WALCOTT'S MEGAFOSSILS. Walcott interpreted most of his Precambrian megafossils as being Paleozoic-like. Once he established a Precambrian age for the Grand Canyon basal complex and correlative units elsewhere in North America, the presence of these fossils seemed to indicate that complex biological forms evolved earlier than previously believed. The fossils were identified as pteropods referred to *Hyolithes* (Walcott, 1883), a fragment of a trilobite and a *Lingula*-like brachiopod (Walcott, 1886b), and a brachiopod related to *Acrothele* (Walcott, 1899). None of Walcott's Precambrian megafossils are considered valid today. His "pteropods" were retracted (Walcott, 1899) as being probably of "mechanical origin." The presumed trilobite, although originally described as belonging to "a genus allied to the genera *Olenellus*, *Olenoides*, or *Paradoxites*" (Walcott, 1886b, p. 43), was later dismissed as an erroneous classification (Walcott, 1899), but, by Walcott's wording, not completely rejected. Ford & Breed (1977) interpreted Walcott's retractions as definite reassignments to inorganic status and so dismissed all of these fossils. Ford & Breed (1977) also reexamined Walcott's *Acrothele* and declared it to be inorganic. The "small *Lingula*-like shell" (Walcott, 1886b, p. 43) is never again referred to in the literature and, in the absence of a specimen, it, too, has been dismissed (Ford & Breed, 1977).

THE PSEUDOFOSSILS AND THE AGE OF THE SUPERGROUP. This paper contains a separate section on Grand Canyon pseudofossils, but the Walcott pseudofossils have been mentioned here because as "true" fossils they played a special role in early efforts to correlate the late Precambrian strata of North America. Most of the genuine fossils of the Grand Canyon Supergroup fall in the category, "problematica." Although some workers will remark that the algal-like forms should be treated botanically, there is still sufficient uncertainty in the taxonomy of these forms to simply call them "fossils *incertae sedis*." In any case, the genuine Supergroup fossils serve to support non-paleontological methods of dating these rocks. The Supergroup pseudofossils only coincidentally pointed contemporary workers to the Precambrian.

Walcott's Paleozoic-like problematica contributed to some confusion between stratigraphic and biologic age determinations of the Supergroup, confusing even Walcott at first. But once the Precambrian age of these strata was established by Walcott, and sustained by his contemporaries, Walcott's reports of Precambrian megafossils were cited without question by later workers. By the 1930s, though, some doubts were beginning to arise about the biologic origin of at least some of the Precambrian animal fossils, including those from the Grand Canyon (cf. Raymond, 1935). Still, continued references to Walcott's fossils perpetuated the belief that complex Precambrian biotas existed. On the other hand, Hinds (1940), at the conclusion of his

studies of the "Beltian" strata of North America, tried to circumvent the problem by *provisionally* raising all of these rocks into the lowermost Paleozoic. (The time-stratigraphic term "Beltian" was, until recently, applied to the Grand Canyon Supergroup and other presumably correlative strata of North America. It should not be confused with the current stratigraphic definition of the northern Cordillera's Belt Supergroup.) Furon (1965) placed all Beltian rocks, including the Grand Canyon Supergroup, in the "Infracambrian" period. More recently, definitive dating of the Grand Canyon Supergroup through radiometric methods and paleomagnetic correlation has shown these strata to range in age from ~823 m.y. to ~1.4 b.y. old (Elston & Grommé, 1974a,b; Elston & McKee, 1982). This age range is within the late Precambrian time frame, or Precambrian Y of U.S. Geological Survey nomenclature. None of the known late Precambrian fossils of the Supergroup so certainly date these strata, but neither do they contradict the dates determined by the non-paleontological methods.

CHUARIA WALCOTT, 1899. In 1883, Walcott noted a peculiar "Discinoid" fossil in the Chuar Group; the fossil was named by him in 1899 as the new genus and species *Chuarina circularis* (Fig. 4). Formally described as "circular disc-like bodies . . . which appear to be the remains of a compressed conical shell" (Walcott, 1899, p. 234), this curious fossil has for more than a century been a persistent taxonomic problem. Probably first alluded to by Powell (1876) and White (1876) from the Grand Canyon, *Chuarina* was first figured (but not named) by Wiman (1894) from late Precambrian Swedish specimens (= *Chuarina* "*wimani*" Brotzen, 1941, the only other species to be included in *Chuarina*, but which Ford & Breed, 1972b, synonymized with *C. circularis*). Walcott (1899) referred to Wiman's publication, but he was not sure of the taxonomic relationship between his *Chuarina* and Wiman's fossils. Since 1876, *Chuarina* has been reported in more than 100 references, recorded from localities around the world, and identified under a perplexing list of specific and generic synonyms and descriptive terms. It has been reported from North America, Europe, the U.S.S.R., and India. Chapman's (1929) identification of Australian *Chuarina*-like markings as "primitive brachiopods" are probably inorganic features produced by weathering (Rowell, 1971). Now known by 12 synonymous species in eight synonymous genera, and by more than 30 nonspecific descriptions, *Chuarina* remains a monospecific genus. The various conspecific names of *C. circularis* Walcott are presented in the list on the following page. An early list of synonyms was presented by Ford & Breed (1973b). For a complete list that includes the nonspecific descriptions and a literature history of all of these names, see Spamer (1984, pp. 158-171).

In terms of affinity to invertebrate and protist taxa, *Chuarina* has been identified as trilobite eggs (as first described by Wiman, 1894,

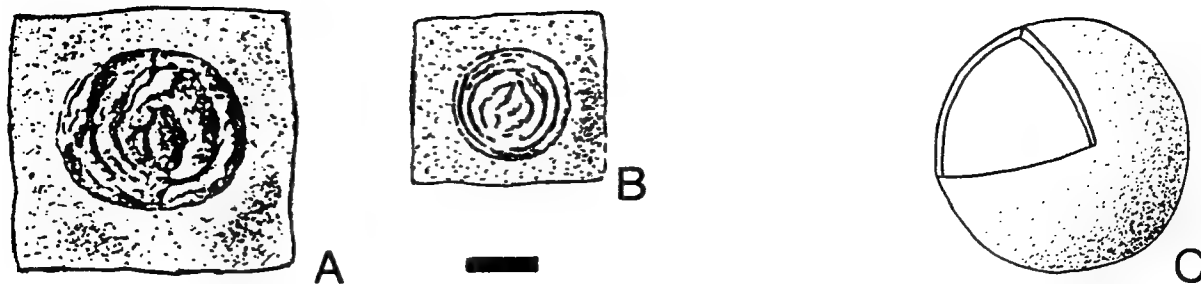


Figure 4. *Chuar* *circularis* Walcott. A, B: Specimens from the type lot (USNM 33800), collected by C. D. Walcott in 1882 some 30 ft (9 m) from the top of the Awatubi Member(?) of the Kwagunt Formation (Chuar Group), on the east(?) side of Nankowep Butte (cf. Ford & Breed, 1972a) (A, B after drawings in Walcott, 1899, pl. 27, figs. 12, 13, respectively). Scale bar measures 1 mm. Note wrinkled discoidal appearance resulting from compaction of originally spherical form. C: Restoration of *Chuar* *circularis* with section showing wall structure of spheroid (after Jux, 1977, fig. 2). Wall structure contained few pores but was thin enough to allow germination by means of permeation (Jux, 1977).

and revived by Regnéll, 1955), brachiopods (including new genera *Fermoria* Chapman, 1935; *Protobolella* Chapman, 1935; and *Vindhyanella* Sahni, 1936), gastropods, ostracodes, foraminifera, hystrichosphaerids, and algae (including new genus *Krishnanella* Sahni & Shrivastava, 1954). *Chuar* or its synonyms have even been placed in new taxonomic families: *Fermoriidae* Sahni, 1936 (*incertae sedis*), and *Chuariidae* Wenz, 1938 (Gastropoda). Ultimately, Ford & Breed's studies (culminating with Ford & Breed, 1977) led them to believe that *Chuar* is "probably a megasphaeromorphic acritarch," an analysis that has not been refuted. ("Acritarch" is a term with compound Greek roots meaning "of uncertain origin.")

In the Grand Canyon Supergroup, *Chuar* is not known to occur below the Chuar Group (Ford & Breed, 1973b, 1977). A *Chuar*-like fossil is reported from the basal formation of the Supergroup (cf. White, 1928b), but neither the specimen nor the locality can be found for verification (Ford & Breed, 1973b). The apparent great length of time represented by the Supergroup (cf. Elston & McKee, 1982) casts doubt on the long-time survival of a morphologically unchanged monospecific algal genus.

Synonyms of *Chuar* *circularis* Walcott, 1899

- Beltanelliformis brunsae* Menner in Keller, 1963
- Beltanelloides sorichevae* Sokolov, 1965
- Chuar* *wimani* Brotzen, 1941
- Fermoria capsella* Chapman, 1935
- F. granulosa* Chapman in Fermor, 1933; *nom. nud.*
- F. minima* Chapman, 1935 (= *Neobolus minima* Chapman in Fermor, 1932; *nom. nud.*)
- F. tripartita* Chapman in Fermor, 1933; *nom. nud.*
- Kildinella magna* Timofeev, 1969
- Krishnanella acuminata* Sahni & Shrivastava, 1954
- Trachysphaeridium vetterni* Timofeev, 1969
- Vindhyanella jonesi* (Chapman) Sahni (1936)
(= *Protobolella jonesi* Chapman, 1935;
= *Obolella jonesi* Chapman in Fermor, 1933,
nom. nud.)

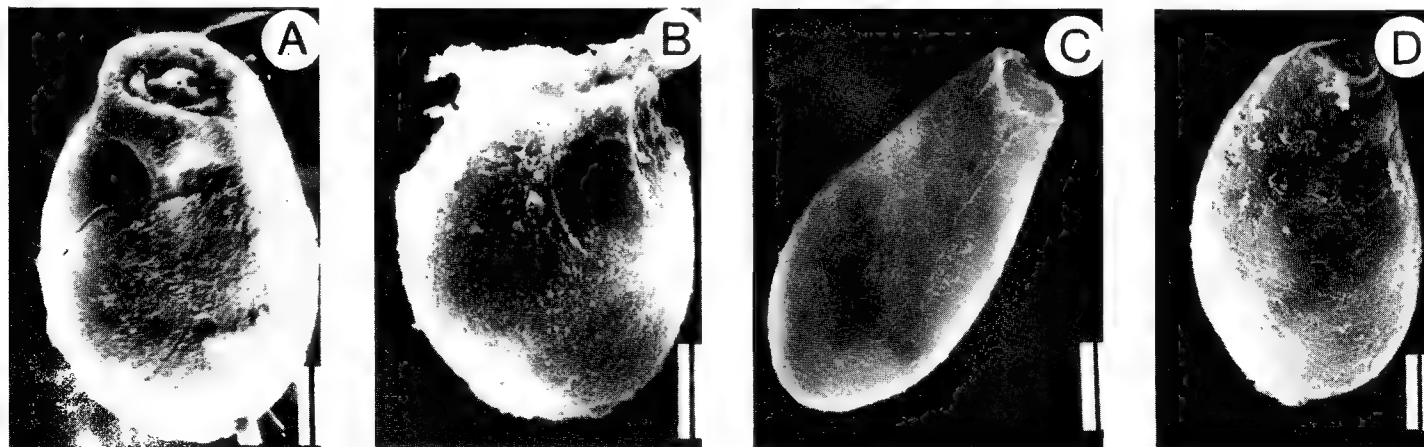


Figure 5. Scanning electron micrographs of *Melanocyrrillium* Bloeser, spp. Specimens are from acid-resistant residues, fine-grained black shale facies of the late Precambrian Walcott Member of the Kwagunt Formation (Chuar Group) on the northern flank of Nankowep Butte. Scale bars measure 25 μ m. All specimens are in the University of California at Los Angeles (UCLA) Paleobiology Laboratory collections. A, UCLA 58962; B, UCLA 58964; C, UCLA 58971; D, UCLA 58979. (Courtesy of B. Bloeser, UCLA.)

MELANOCYRILLIUM BLOESER, 1985. Another problematical late Precambrian fossil has recently come to light; this is *Melanocyrrillium* Bloeser, 1985 (Fig. 5). It was first identified by Bloeser *et al.* (1977) in the Chuar Group as a form of chitinozoan. Later, it was determined to be a new genus of uncertain affinity, first recorded as such in an abstract by Bloeser (1979) as three (named) new species of a new genus, *Melanocyrrillium* [sic; nom. nud.]. [Bloeser (personal communications, 1983, 1984) has graciously permitted me to read her manuscript and cite her new genus and species; the formal descriptions are in press in the *Journal of Paleontology* for 1985. The species are *M. hexodia-dema* (designated the genotype by Bloeser), *M. fimbriatum*, and *M. horodyskii*. All of these names were proposed by Bloeser (1979) but are, of course, *nomina nuda* there and in the present paper.]

In Bloeser's (1985) formal description, *Melanocyrrillium* is interpreted as an encystment stage of an unidentified alga. One specimen from the Grand Canyon was figured by Vidal (1984, p. 56, lower two figs.) as a "representative of an abundant type of plankton that appeared in shallow coastal waters roughly 800 million years ago", and that "the cells, which were presumably heterotrophic eukaryotes, [may have] moved by means of undulipodia (the eukaryotic equivalent of bacterial flagella)." (Eukaryote, or nucleated, cells appear to have evolved from prokaryote cells [lacking nuclei] as unicellular plankton about 1.4 b.y. ago. Loosely colonial eukaryote microorganisms are also known from rocks about that old [cf. Vidal (1984)]. Heterotrophic cells consume organic substances [conversely, autotrophic cells ingest inorganic nutrients]; they represent the most advanced kinds of planktonic organisms.)

Melanocyrrillium is strictly microscopic, yet unlike the micro- to macroscopic *Chuar* our understanding of it is not clouded by decades of confusing synonymies. It has been identified from localities around the world by such descriptions as "flask-," "bag-," or "vase-shaped" microfossils and has been noted in at least 12 publications dating to 1977 (cf. Spamer, 1984; Bloeser, 1985). Studies of this new and peculiar genus have only just begun.

OTHER MICROFOSSILS. Other microorganisms of the Grand Canyon Supergroup are neither well known nor much discussed in the literature. Downie (1969) remarked on a variety of round or oval microfossils in the Chuar shales; they were noted to resemble most of the species recorded by Timofeev (1960, 1966) from the late Precambrian beds of Sweden. But, Downie observed, none of the species can be used as an index fossil because they also have been seen in Early Cambrian rocks.

At the base of the Walcott Member, Schopf *et al.* (1973) found well-preserved filaments and

spheroids that were the first nonstromatolitic community of microorganisms to be reported from any Precambrian rock. Some of the filaments, these authors stated, are indistinguishable from *Eomycetopsis* of the Bitter Springs Formation of Australia and similar filaments from Greenland. The fossils are all restricted to the late Precambrian and, if they are determined to be synonymous taxa, they may represent an index fossil. They are primitively organized and "could pre-date, perhaps substantially, the emergence of megascopic, multicellular life" (Schopf *et al.*, 1973, p. 1321).

Bloeser (verbal commun., 1983) has reported a very interesting relationship--an association of *Melanocyrrillium*, *Chuar*, and "as yet unnamed single spheres and colonial aggregates of sphaeromorphs," all well preserved in shales of the Walcott Member (Kwagunt Formation, Chuar Group). Earlier studies have had the luxury of discussing collections mostly of single kinds of microfossils, but the interrelationships of several problematical taxa is something which future work must now take into account. The paleoecological implications of the recent discovery are still under study, but the Walcott shale environments were clearly ideal for the coexistence (multibiosis?) of several complex forms of premetazoan organisms.

Bloeser (verbal commun., 1983) has also said that she has found well-preserved spheroids, filaments, and colonial aggregates of single-celled organisms in silicified chert nodules of the Carbon Canyon Member (Galeros Formation). This occurrence represents a significantly different microfossil assemblage than those previously reported. (Microfossils in black chert nodules of the Carbon Canyon Member were first noted in an abstract by Schopf *et al.*, 1974; they were identified only as "stromatolitic biotas." The colonial aggregates were at that time either unknown or intentionally not mentioned.) The Galeros colonial aggregates are in clusters averaging five cells, but some rare colonies contain up to 30 cells. Most occurrences, however, are as single thin-walled cells; together with the colonial aggregates, they tend to show interesting prokaryote/eukaryote transitional relationships. As noted earlier, though, singular and colonial eukaryote cells are known from rocks as old as 1.4 b.y. (Vidal, 1984), at least 400 m.y. older than the Chuar fossils; so the Grand Canyon occurrences are not especially significant to studies of evolutionary radiation.

From about 150 ft below the top of the Awatubi Member of the Kwagunt Formation, eukaryotic algal(?) filaments have been described by Horodyski & Bloeser (1983). These are single carbonaceous filaments that occur in a 0.1-mm-thick lamina at one locality on the southwest face of Nankoweap Butte. Although it is "remotely possible" that these microfossils could be worm-like metazoans, an algal affinity is favored by Horodyski & Bloeser on comparisons with other

Precambrian microfossils. Furthermore, the hypersaline shallow-water depositional environment interpreted by Ford & Breed (1973a) would have been more likely to support and preserve an influx of such significant numbers of "buoyant alga stipes" rather than worm-like metazoans (Horodyski & Bloeser, 1983).

Less-certainly-algal filaments are found with stromatolites of the Unkar Group's Bass Limestone (Dalton, 1972; Dalton & Rawson, 1974; Beus *et al.*, 1974). In association with these filaments are ovoid pellets that could indicate the presence of a boring organism that lived symbiotically with the algae (Dalton, 1972). Ford & Breed (1977) pointed out that no burrows are seen in the Bass, but hypothesized that the ovoid particles could be fecal pellets of the infaunal organism.

Forty feet above the base of the Bass Limestone, along Bass Trail, Smith (1969) observed a 4- to 8-in.-thick zone of "apparently bivalved fossils" of unknown affinity. S. Beus (*in Beus et al.*, 1974, p. 51) thought these were "oncolites or other algal structures."

STROMATOLITES. Dawson (1896) formally described Walcott's (1883, 1890b, 1894, 1895) "Stromatopora-like forms" and "concretionary limestones." Attributing them to a new species, *Cryptozoon occidentale*, Dawson hoped that better specimens would be found later. Even so, these fossils seemed to paleontologically correlate the Precambrian strata of the Grand Canyon with other Precambrian formations of North America, reinforcing the interpretations already made by Walcott. But stromatolitic forms have traditionally been taxonomically controversial, and just three years later Walcott (1899) expressed some doubt about Dawson's assignment by listing the fossil as *Cryptozoon? occidentale*. In 1914, Walcott reassigned *C. occidentale* to his new genus, *Collenia*, but Rezak (1957) referred the species back to *Cryptozoon* Hall, 1884. Häntzschel (1962) applied the general name Stromatolite [Stromatolith] Kalkowsky, 1908, to both *Cryptozoon* and *Collenia*, remarking that they are "differentiated only on the basis of general form;" he noted, too, that some workers have even regarded them as inorganic. (Stromatolites are not considered by Häntzschel, 1975.) Raymond (1935, p. 377) did not believe that the algae of the Grand Canyon and other Precambrian localities were organic, citing "very similar concretions" reported by Olaf Høltedahl. "At least," Raymond concluded, "there is no excuse for applying generic and specific names to these indescribable objects." Still, the name *Cryptozoon occidentale* has intentionally appeared as a taxonomically specific identification as late as 1966 (*cf.* Sen, 1966), and a paleontological index (Sastri & Gururaja, 1980) lists the species as an apparently valid paleobiological taxon.

Johnson (1961) discussed the limestone-building algae, into which category the stromatolites fall. Both *Cryptozoon* and *Collenia* are

classified by Johnson under the Phylum Schizophyta (Falkenberg) Engler, 1892, Class Schizophyceae Cohn, 1880, "Section" Spongiostromata Pia, 1927 [quotation marks are Johnson's], Division Stromatolithi Pia, 1927. The "Stromatolithi" are said to be all those forms that grew attached to the substrate; the "Oncolithi" are the unattached forms. Johnson referred to the Stromatolithi and Oncolithi as Subsection groups. He recognized and described both *Cryptozoon* and *Collenia* and referred to "*Cryptozoon occidentales* [*sic, nom. null.*] Dawson" from the late Precambrian Missoula Group of Montana (Johnson, 1961, pls. 91, 115). The Grand Canyon as a locality is mentioned by Johnson in passing (p. 246), where he noted only that stromatolitic forms attributable to blue-green algae are found there. Johnson did remark in general, however, that "The Precambrian limestones are built largely by the genus *Collenia*, while those of the Cambrian include forms of both *Collenia* and, particularly during the Late Cambrian and earliest Ordovician, the genus *Cryptozoon*" (p. 256).

Stromatolites are rather common in the Chuar Group, having been noted therein since Walcott's early studies of these strata. In 1930, a brief reconnaissance of the Chuar strata in easternmost Grand Canyon (Resser, 1930, 1931) noted several beds that are so dramatic in appearance that they obviously are Walcott's stromatolite localities. The investigators also found seaweed-like algae, "but unfortunately no trace of animal remains" (Resser, 1930). Ford & Breed (1969, 1972a, 1973a) succeeded in stratigraphically locating Walcott's various stromatolite beds. These beds are at the base of the Jupiter Member, in the upper part of the Carbon Canyon Member (both in the Galeros Formation), and at the base of the Awatubi Member (Kwagunt Formation). Ford & Breed (1973a, p. 1257) expressed confidence that "*C. occidentale*" is from the "spectacular biohermal horizon [of the Awatubi Member] around Nankoweap and Carbon Buttes."

Each of the three Chuar stromatolite beds is characteristically distinct, but each is "predominantly undulating dome-shaped" (Ford & Breed, 1973a, p. 1257). Ford & Breed (1977) also remarked that the stromatolites resemble or approach the form-genera *Inzeria*, *Stratifera*, *Baicalia*, and *Boxonia*, all of which correlate with the Upper Riphean (late Precambrian) of the U.S.S.R., reaffirming Chuar paleomagnetic and radiometric age determinations.

Stromatolites of the Grand Canyon Supergroup can also be seen in the Comanche Point Member of the Dox Formation (Unkar Group); they represent the only fossils in that formation (Stevenson & Beus, 1982). These investigators remarked only that the Dox stromatolites occur as "laterally linked hemispheroids" (p. 169) and that the bed is "interpreted as an intertidal or supratidal salt flat subjected to periodic desiccation" (p. 170). This interpretation parallels Ford & Breed's (1977) observations that the Chuar Group

stromatolites seem to have been built up in quiet, shallow waters with intermittent desiccation.

Minor algal laminations have been noted in the Carbon Canyon and Walcott Members (Chuar Group) (Ford & Breed, 1973a), and miscellaneous stromatolitic units have been seen in the Bass Limestone (Unkar Group) (White, 1927a, 1928b, 1929b; Shride, 1967; Nitecki, 1971; Beus *et al.*, 1974). (White, 1929b, p. 392, thought that some of the Bass stromatolites could be "the work of bacteria related to *Crenothrix*.")

Noble (1914, p. 41) remarked that the Unkar Group was "destitute of fossils or of other evidence of life." However, in his measured section of the Bass Limestone in Hotauta Canyon, he noted in a white limestone "nodules resembling Cryptozoon" (p. 45) and, in the basal white limestone, "chert . . . nodules having a roughly concentric structure somewhat suggestive of the structure of Cryptozoon" (p. 46). Whether Noble in fact observed the Bass stromatolites is a matter of conjecture. The record indicates that he suspected a biogenic presence in these rocks, but he apparently was unsure enough to assert the premise. Because Noble's study was made in the Shinumo area of the Grand Canyon, he could not remark on the stromatolites that we now know exist in the Dox Formation in the Vishnu Temple quadrangle, although he did measure a partial stratigraphic section of the Dox in his study area.

As a final note on Precambrian algae (although not stromatolitic), White (1929b, p. 392) reported that "Markings difficult to explain except as impressions of algal thalli were found abundantly in silty shales near the top of the Hakatai shale."

PALEOBIOLOGICAL STUDIES. Until recently, the late Precambrian strata of the Grand Canyon were important as parts of larger studies of North American stratigraphic correlation. The fossils --real and presumed--were relied upon as special indicators of the Precambrian age of the sediments, without particular regard to their paleoenvironmental significance. But once the different megafossils began to be recognized as inorganic features, and once the paleoenvironmental lithologies of the formations began to be studied, it became evident to paleobiologists that the record of the rocks in the Grand Canyon Supergroup is more complex and more interesting than previously believed--something worthy of more intense investigation. The history of premetazoan life on earth has been advanced partly through discoveries in the Grand Canyon. In turn, feedback from paleobiological studies in other late Precambrian strata around the world is now enabling researchers to better fit the Grand Canyon strata into the world picture of early life.

A. Seilacher's recent preliminary reinterpretation of the peculiar late Precambrian Edia-

cara-type fauna found at various world localities (see Seilacher, 1983, and Lewin, 1984) sees these fossils as belonging to an extinct fauna *not* ancestral to the groups that explosively diversified during Cambrian time. What implications this hypothesis may have toward interpreting the late Precambrian Grand Canyon paleofauna, including possible trace fossils, remains to be seen. The hypothesis is quite intriguing and awaits more intense investigation and testing around the world.

Recently, Miller & Byers (1984) called for a reinterpretation of early Paleozoic community structures, a reinterpretation that also has bearing on the late Precambrian faunas. These authors pointed out that "An abundant early Paleozoic infauna is indicated by bioturbated zones and diversity of deposit-feeder and suspension-feeder trace-fossil genera" (p. 40). This evidence conflicts with the record of the shelled fauna, which at that time lacked infaunal members. Of course, some trace fossil genera are found in both Precambrian and Paleozoic sediments, and Miller & Byers included in their Table 1, without further remark, the late Precambrian Shinumo Quartzite (known only in the Grand Canyon) as a highly burrowed quartz arenite; they cited their source as "W. C. James, 1982, personal communication." This is an interesting paleontological observation, one that has not been noted in the literature. If the Shinumo is indeed bioturbated, that formation is the oldest of the Grand Canyon fossiliferous strata excepting the algal remains of the underlying Hakatai Shale and Bass Limestone. Naturally, this pronouncement is presented with caution. Miller & Byers (1984, p. 42) stated, citing several references, "There is considerable debate over the age of the oldest trace fossils . . . , but there is consensus that trace fossils constitute the earliest record of metazoan life and that traces of deposit feeders in Precambrian strata predate both body fossils of shelled animals and arthropod trace fossils" Miller & Byers concluded (p. 42):

"We reject the notion that infaunal burrowing and bioturbation were minimal in the early Paleozoic. * * * We stress that many of the early Paleozoic infaunal traces were produced, as they are today, by animals with little chance of fossilization. The history of infaunal habitation is written in the sediments, not in the body-fossil record. When bivalves, for instance, began in the late Paleozoic to burrow deeply, they were radiating into a new habitat for their taxon, not invading an azoic ecospace."

Although Miller & Byers elaborated only on the early Paleozoic infaunal record, they did recognize that evidence of deposit-feeding infaunal animals is also found, with less frequency, in Precambrian rocks. The paleobiological implications made by these authors clearly can be ap-

plied to late Precambrian faunas of all localities, including the Grand Canyon. Some Precambrian fossils have been declared to be pseudofossils--and perhaps rightly so--but now they might warrant reexamination in light of these new insights on the possible nature of some early life forms. (Later in this paper, in the section on pseudofossils, some additional problematical fossil forms of the Grand Canyon are discussed.)

The different algal problemata of the Grand Canyon Supergroup (*Chuar*, *Melanocyrtium*, and the various spheromorphs and filaments) are beginning to teasingly reveal paleoecological relationships that are more complex than previously believed. Exquisitely preserved *Melanocyrtium* occur in teeming abundance in the fine-grained black shale facies of the Walcott Member (approximately 10,000 specimens/cm³; cf. Bloeser *et al.*, 1977; Bloeser, 1985) in association with cyanophyte spheroids and microphytoplankton (Bloeser, 1985). This community of fossils, Bloeser (1985) suggested, could represent a true community of late Precambrian organisms, living in a restricted environment, and not simply an aggregation of microscopic body fossils brought together by physical processes.

Chuar appears to have at last survived paleobiologists' attempts to discard it as inorganic (the last being by Häntzschel, 1962); but its true biologic nature has yet to be satisfactorily established. Ford & Breed's studies of this problematical form positioned it definitely among the true fossils, albeit of uncertain paleoecologic position. Ford & Breed (1977, p. 172) speculated, without further remark, that it could have been "the metabolic stimulant food for the metazoan animals that were evolving then," and Jux (1977) suggested that it may have been a cold-water organism. Bloeser's observation of the more-studied *Chuar* in association with the less-studied *Melanocyrtium* is bound to influence world-wide paleoecological interpretations of both genera. Even more critical to future studies may be the inferences concerning the colonial aggregates. Bloeser's (1985) initial study of *Melanocyrtium* is fortuitously unbiased by comparisons with associated microfossils, so her report should prove to be a solid reference from which future paleoecological studies can extrapolate.

The unilateral interpretation of *Melanocyrtium* specimens as the possible encystment stage of an unidentified alga (Bloeser, 1985) cannot yet be contended because the interpretation has only just been presented. But the known size range of the genus (32-170 μ m; Bloeser, 1985) reinforces such an interpretation. The reported size range of *Chuar*, however, makes any unilateral biological interpretation of *Chuar* difficult to perceive. As *Chuar* or one of its synonyms, this fossil has been noted in the literature to have a diameter as large as 44 mm (!), but specimens are more commonly reported between 2-5 mm (like those from the Grand Canyon), with

others measuring only a few microns in diameter (Ford & Breed, 1977). Although Vidal (1974) considered *Chuar* to be polymodal, suggesting that upper and lower size limits in a taxonomic definition of the genus are inappropriate, he admitted to having problems in believing that the very large forms were actually *Chuar*. Bloeser (verbal commun., 1983) has concurred that the very large *Chuar*-like forms, particularly, are difficult to accommodate under the genus.

AFTERWORD. So, what can be inferred from the apparently rich diversity of late Precambrian fossils of the Grand Canyon? At this time, relatively little. These enigmatic organisms of such interesting variety and paleobiologic complexity are food for academic thought. Although stromatolites were well along the evolutionary road by the time the sediments of the Grand Canyon Supergroup were laid down, many of the planktonic prokaryote and eukaryote organisms were in the early stages of development--and the heterotrophic eukaryotes first appeared at about the same time the *Chuar* Group sediments were deposited. The organisms now known as *Melanocyrtium* are, according to Vidal (1984), among the first heterotrophic plankton. Still, the rocks of the *Chuar* Group, and perhaps those of the whole Grand Canyon Supergroup, are teeming with other unstudied, probably unknown, organisms. Studies will be slow in coming, but they will by no means be unwelcome. There is much to be explored in what Vidal (1984, p. 57) called "the golden age of unicellular life." But a bioturbated Shinumo Quartzite, well down in the strata of the Grand Canyon Supergroup, may well be another enigma for Grand Canyon paleobiologists to ponder. This formation predates Vidal's "golden age" strata, and yet we must infer that bioturbation represents an active or abundant metazoan infauna. I hesitate to accept the Shinumo trace fossils from an unverified second-hand source; but I am not surprised that the Grand Canyon is still telling us, more than a century after Walcott, enigmatic tales of life on earth. There is, indeed, still much to be explored.

Paleozoic Invertebrates

Paleozoic invertebrate taxa comprise the majority of Grand Canyon fossils. They are reported and discussed in so many publications that even a species list would be lengthy. For the sake of brevity, a treatment of the paleoecological relationships of the Grand Canyon invertebrate faunas is avoided here. Instead, the chronology of invertebrate studies in the Grand Canyon is reviewed, briefly examining the roles the fossils have played in unraveling the geologic history of the region and their contributions to the development of geologic principles.

Invertebrate fossils have been collected from Grand Canyon stratigraphic units outside of the Grand Canyon since the 1850s (e.g., Blake, 1856;

Marcou, 1858), but, as mentioned earlier, the first fossils from the Canyon-proper were described by Newberry in 1861. In the early stratigraphic studies of the Grand Canyon region, particularly before the 1930s, invertebrate fossils were used as indices to relative age and, together with lithology, as clues in the synthesis of paleogeography. The concept of facies (as we now understand them) had not yet been developed. Lateral variations in lithology and fossil assemblages, as meticulously noted by earlier workers, became critical data to later researchers who recognized the significance of facies. In fact, the depositional sequences and exposures of the Grand Canyon are so well defined that it was in these rocks that the modern concept of facies and the principle of key-bed correlation were first developed and tested.

The following subsections will discuss the Grand Canyon's Paleozoic sequence of strata from the Early Cambrian to the Early Permian. Although the Cambrian strata are not the most thoroughly studied of the Grand Canyon's formations (the higher Permian strata have that distinction), the stratigraphic principles of key beds are best illustrated by the studies of the Cambrian Tonto Group. For this reason, the Cambrian subsection of this paper (below) elaborates more on historical development than do subsequent portions of this section.

CAMBRIAN. The Tonto Group was named by Gilbert (1874) from the Tonto Basin of south-central Arizona. Gilbert soon correlated the Tonto Group with similar rocks exposed near the bottom of the Grand Canyon (Gilbert, 1875). In 1879, Charles D. Walcott began his tenure with the U.S. Geological Survey by spending part of the summer studying the stratigraphic sequence exposed through Kanab Canyon. He quickly concluded that Gilbert's Cambrian age for the strata was a correct assignment (*i.e.*, Gilbert's and Walcott's "Primordial Silurian") (Walcott, 1880; see also Nelson & Yochelson, 1980). Walcott based his conclusion on the stratigraphic distribution of diagnostic genera of brachiopods and trilobites. He sustained this view in subsequent research in the easternmost Grand Canyon (Walcott, 1883), and specifically ascribed these strata to the Cambrian (actually using that term).

In 1886, Walcott published the first of his ambitious syntheses of North American Cambrian history (Walcott, 1886a,b). On the basis of biostratigraphic correlation, the Tonto Group of the Grand Canyon was placed in the Late Cambrian. (His correlation charts, however, continued to show the pre-Tonto rocks of the Grand Canyon Supergroup as partly if not wholly Early Cambrian, although in the text of these publications he removed these strata to the Precambrian.) On the basis of "subfaunas," Walcott (1891a,b) tentatively referred part of the Grand Canyon Cambrian strata to the Middle Cambrian. He alluded (1891b, p. 235) to a study of the Tonto Group fauna in preparation, but such a comprehensive survey was

never published by him.

By 1908, the Tonto Group of the Grand Canyon had been placed wholly into the Middle Cambrian (Walcott, 1908, p. 167). Noble (1914), however, cautiously pointed out that although the Bright Angel Shale contained Middle Cambrian fossils, the underlying evidently unfossiliferous Tapeats Sandstone was either Middle or Early Cambrian. (We now recognize that the stratigraphic time lines within the Tonto Group diagonally cross the lithologic boundaries within the strata.) Noble (1914) correlated the unfossiliferous Muav Limestone of the Shinumo area to the equivalent Middle Cambrian fossiliferous stratum at Kanab Canyon. Ransome (1917) adopted Noble's paper as a Grand Canyon standard in a correlation of the Paleozoic strata of Arizona.

Schuchert (1918b) was more emphatic in declaring that no Early Cambrian rocks were known in the Grand Canyon, although it is apparent from his text that he was encouraged by discussions with Noble to make such a pronouncement. He briefly mentioned the presence of various kinds of brachiopods and trilobites, but recognized that in these rocks *Dolichometopus* was the most reliable tool for biostratigraphic correlation. Schuchert indirectly reported that Noble had raised the Muav Limestone to the Late Cambrian, based on sparse collections of fossils, a conclusion that Noble tentatively formalized in 1922. It is Noble's (1922) study of the Paleozoic formations exposed along Bass Trail that includes the first comprehensive faunal lists from various Cambrian localities in the Canyon. Although age determinations based on these fossils remained problematical for years afterward, the usefulness of the faunal lists permitted the first correlations of strata between several localities throughout the Canyon.

The year 1931 was a turning point in Grand Canyon Cambrian geology. McKee (1931), in *Grand Canyon Nature Notes*, a folksy periodical once published at Grand Canyon, wrote a short article on the Cambrian geography of the Grand Canyon region as interpreted from the fossils. This was the inaugural paper of a growing research interest that would eventually lead to McKee & Resser's (1945) authoritative monograph on the Grand Canyon Cambrian.

At the 16th International Geological Congress, held in 1933, a theory of cyclic sedimentation was formulated, called the "pulsation theory." This hypothesis maintained that rhythmic transgressions and regressions occurred worldwide throughout the Paleozoic. This doctrine was elaborated upon by Grabau (1936), who relied in part upon the Grand Canyon Cambrian succession of strata to illustrate his interpretation of the hypothesis. He included species lists for various localities in the Canyon and considered the lower two formations to be Middle Cambrian in age; but he thought that the Muav Limestone was Late, possibly Middle, Cambrian. [Grabau (pp.

573 ff.) referred to undefined "Nunkoweap shales of Grand Canyon." He recorded only *Anoria tontoensis* (Walcott) in these rocks. These "Nunkoweap shales" appear to be undivided strata of the Tonto Group in the Nankoweap area of eastern Grand Canyon, but they probably refer specifically to the Bright Angel Shale.]

Stoyanow (1936) presented a definitive correlation of the Arizona Paleozoic formations in which he declared the whole Tonto Group to be Middle Cambrian in age, based on paleontologic criteria. His assignment of the Muav Limestone to the Middle Cambrian was not positive, however, because he was unable to correlate Late Cambrian fossils with those of the Muav.

Also in 1936, a preliminary geological report on the Tonto Group was published by Wheeler & Kerr. They studied only three sections--Pierce's Ferry (extreme western Grand Canyon), below Yavapai Point (at Grand Canyon Village), and Tanner Canyon (easternmost Grand Canyon)--but were able to see in that piecemeal view some important characteristics which laid the foundations for our present understanding of the Tonto Group. Most important among the observations was the discovery of the diagnostic Early Cambrian trilobite *Olenellus* Hall in the Bright Angel Shale at Pierce's Ferry. At the other two localities, however, the Bright Angel fauna was characteristically Middle Cambrian. Wheeler and Kerr succinctly remarked, "... the problem of the Tonto has become more complex" (p. 13). These investigators considered the fossils in the Muav Limestone to be Middle Cambrian. They cited a 1935 personal communication from C. E. Resser, who declared that the Middle Cambrian trilobite *Kootenia* was "the characteristic fossil of the Muav" (p. 14).

With the stage thus set by more than 60 years of study and opinion on the Tonto Group, the time was right for the first exhaustive survey of the Grand Canyon Cambrian. That survey was conducted under the auspices of the Carnegie Institution of Washington, when Park Naturalist Edwin D. McKee and field assistants began a systematic reconnaissance of all of the Paleozoic strata throughout the Grand Canyon (for progress reports, see McKee, 1937a, 1938b, 1939, 1940; Merriam, 1941, 1942). Fossil collections were assembled and a picture of paleontological zones and lateral lithologic gradations began to emerge; the modern concept of facies began to take shape. (These concepts were first applied by McKee to the Kaibab and Toroweap Formations. These strata will be discussed in a later subsection.)

In 1942, Schenk & Wheeler published their study of the Cambrian strata of western Grand Canyon. These workers had stratigraphically and paleontologically correlated the western Grand Canyon Cambrian strata with those of southern Nevada, in the process discarding the Bright Angel Shale and Muav Limestone in the western Grand Canyon in favor of formations named in the

Muddy Mountains section to the west. The "Mead Limestone," newly named by Schenk & Wheeler, is equivalent to what now are called unclassified dolomites that unconformably overlie the Muav Limestone. Although all attempts to date the supra-Muav unit have thus far failed, it is thought to be Late Cambrian in age (Billingsley, 1978) or ?Cambrian-?Devonian (Beus, 1980).

In 1943, McKee & Resser's (1945) classic monograph, *Cambrian History of the Grand Canyon Region*, was approved for publication by the Carnegie Institution of Washington. The monograph produced a benchmark for all subsequent studies on the Tonto Group. The stratigraphy and ecology was worked out by McKee, supplemented by a comprehensive review of the Cambrian fauna by Resser. Basically, the publication revealed that the Tonto Group included "numerous widespread fossil beds, thin but persistent conglomerate zones, and horizons of distinctive lithology that serve as reliable key beds . . ." (p. 1). The transgressions of the Cambrian sea, from west to east, took place in pulses, separated by periods of eustatic stability during which uniform sedimentary deposits were laid down. Temporary regressions were quick and were followed by stable periods of continued deposition. Facies, as defined by lithologic and paleontologic composition, are consistent from one transgressive sequence to the next and are traceable through the length of the Canyon. Time planes cut diagonally across the lithologic boundaries; some of these are apparently represented by thin fossil beds that are remarkably persistent through much of the Canyon. Three principle faunal horizons were identified by McKee. These are, in ascending order, the *Olenellus*-*Antagmus* horizon, the *Glossopleura*-*Alokistocare* horizon, and the *Solenopleurella* horizon. Only the *Glossopleura*-*Alokistocare* horizon extends through the length of the Canyon; the other two extend eastward only to Granite Park (*Olenellus*-*Antagmus*) and to the area just west of Kanab Canyon (*Solenopleurella*), where they pass into incompatible facies of the Cambrian sea.

McKee also observed that the faunal sequence in the Grand Canyon Cambrian is composed of many genera that have considerable vertical ranges in the strata, but that the species within those genera are relatively short-lived. Laterally, faunal variations are due to facies changes. Resser described from the Grand Canyon Cambrian the following assemblage of fossils: eocrinoids, one genus and species (new species); brachiopods, 14 species (three new) in four genera; gastropods, two species (one new) in two genera; trilobites, 37 species (32 new) in 22 genera (one new); and conchostracids, 23 species (and one new subspecies) in five genera. Also noted were miscellaneous algae and sponge spicules. Most of the fossils had been collected by C. D. Walcott in 1879 and 1882 and by various workers during the 1930s.

Wheeler (1947), elaborating on the Cambrian transgression in the Great Basin and Grand Canyon regions, traced the basal Cambrian deposits eastward from the Nopah Range of southeastern California to Bass Trail in the Grand Canyon. He observed that the time-stratigraphic lines of transgression successively disappeared eastward as the sedimentary units lapped up onto the Precambrian basement complex. Early Cambrian sediments and fauna appear at the basal Cambrian unconformity in the west, while to the east Middle Cambrian and eventually Late Cambrian types appear at the unconformity. *Olenellus* appears at the Nopah Range in a 900-ft-thick zone more than 8,500 ft stratigraphically above the Precambrian unconformity; at Frenchman Mountain, Nevada, the zone is only 32 ft thick and 390 ft above the unconformity; in western Grand Canyon it appears 182 ft above the unconformity; and at Granite Park a "relict fauna" marks the easternmost occurrence of this trilobite. The genus is unknown at Bass Trail. Wheeler (p. 155) confidently declared that "at an unknown point in the Grand Canyon east of Granite Park, the basal sediments of the Cambrian sea were deposited contemporaneously with the terminus of the *Olenellus* zone in this region" He apprised this evidence as a demonstration against the doctrine of diastrophism (in which stratigraphic hiatuses, ostensibly traced worldwide, delineate coincident boundaries in time). The stratigraphic correlation of unfossiliferous formations was practiced on the basis of physical relationships (principally lithology and unconformities), and Wheeler took issue with this method. Where strata are found in one section to be equivalent to a hiatus between two strata in another section, a faunal or time boundary must eventually be selected to separate the units in the more complete section--or a third unit can be proposed. It was this issue that Wheeler addressed in the Great Basin Cambrian. He considered faunal correlation to be "much more precise" than the diastrophic methods of time stratigraphy, and he proposed that the base of the *Olenellus* zone should define the base of the Cambrian System.

In 1948, a conference was held by the Geological Society of America on "Sedimentary Facies in Geologic History." McKee (1949), at that conference, presented several examples of facies changes in Colorado Plateau strata to illustrate the advantages of identifying contemporaneous facies; in part (p. 37):

"A case in point is illustrated clearly by Cambrian deposits of Grand Canyon.... Under the formation name of Bright Angel shale is included a sequence of . . . sediments that are successively younger as determined by fossils, from west to east through the 200 miles of Grand Canyon. In the extreme west the lower part of the formation contains *Olenellus* and therefore is of Lower Cambrian age. In the east, *Glossopleura* and other

Middle Cambrian fossils occur at a corresponding distance above the base. Although the shales are lithologically similar throughout the area . . . , fossils prove that the shale beds actually represent a succession of shale facies of different ages."

The establishment of time-stratigraphic lines through faunal analyses is, in such cases, decisively more practical and advantageous than any such attempt through lithostratigraphic analyses.

In 1951, McNair reviewed the Paleozoic stratigraphy of northwestern Arizona, correlating and reclassifying many of the formations between north-central Arizona and southeastern Nevada. His paper was presented as a compilation of all of the rock systems represented in the region. Fossils are mentioned throughout the text (mostly where identified in measured stratigraphic sections) but McNair did not make much reference to them as stratigraphic markers; and he referred the reader to published works for elaboration on various facies relationships. Much of McNair's ambitious and lithologically well documented stratigraphy has not been upheld in the Grand Canyon (cf. Billingsley, 1978), but his Cambrian stratigraphy in the Canyon was adopted almost wholly from McKee's work there.

Wood (1956, 1966) was the first to expand on the McKee principles of facies analysis in the Tonto Group. Examining the facies changes in the somewhat problematical Muav Limestone, between Diamond Creek in the Grand Canyon and the Yampai Cliffs to the south, he traced to the south and southeast shoreward trends in a Muav sea embayment. The correlation between Yampai Cliffs and the Grand Canyon was, however, accomplished through lithologic details and topographic expression of the beds because the usual trilobite faunas used in Muav correlation are absent in that section. Wood (1966, p. 1235) regarded this faunal omission as "Very probably the . . . consequence of hypersalinity in a shallow sea in a zone parallel to but at some distance from the shore line" However, *Girvanella* was identified and correlated between some localities in the study area.

A comprehensive lithostratigraphic, paleogeographic, and paleoecological survey of the Cambrian units of the craton in the United States was synthesized by Lochman-Balk (1971). In this survey she constructed a succession of faunal-assemblage zones, diagnostic of specific time-stratigraphic units, that can be traced throughout the cratonic and adjoining miogeosynclinal deposits. These assemblage zones are based on a number of trilobite genera associated at different localities. Six stratigraphically contiguous assemblage zones pass through the Grand Canyon. These are, in ascending order: Upper *Olenellus* (late Early Cambrian), *Plagiura-Poliella*, *Albertella*, *Glossopleura*, *Bathyriscus-Elrathina*, and

Bolaspidella (all Middle Cambrian). Not all of these genera are, however, recorded from the Grand Canyon (cf. McKee & Resser, 1945). The problematical undifferentiated dolomites that occur above the Muav Limestone in the Grand Canyon region (?Upper Cambrian by McKee & Resser, 1945; undifferentiated Cambrian by Wood, 1956, 1966; ?Cambrian-?Devonian by Beus, 1980) were tentatively equated by Lochman-Balk to the *Bolaspidella* Zone.

Wanless (1973) presented a critical reevaluation of the depositional environments of the Grand Canyon Cambrian. Based on lithologic and paleontologic evidence, he presented cases for a "Bahama-type, storm-dominated tidal flat" in one western facies of the Muav Limestone (traditionally treated as a more-offshore environment), a tidal flat environment in part of the Bright Angel Shale in central to eastern Grand Canyon, and other shoal water conditions throughout these formations. Paleontologic evidence from some localities included *Scolithus* burrows in both formations and rare stromatolites in the Muav of eastern Grand Canyon. Wanless summarized in his abstract:

"This re-evaluation provides a framework for reinterpreting the remaining bulk of less diagnostic facies comprising the Grand Canyon Cambrian and necessitates that total reconsideration be given to the classic concepts this sequence has so long served to illustrate."

But classic concepts do not succumb quickly or easily to revision. The Grand Canyon literature has not followed up on this interesting, generally well-documented alternate interpretation of the Tonto Group paleoenvironments.

The overall Cambrian-Ordovician transgression observed in North American rocks extends much further inland than would be expected by the single cause of flexural subsidence of sediments and crust in the passive-margin miogeosynclines that encircled most of the continent. Bond *et al.* (1983, p. 779), after noting this phenomenon, suggested that such an enigmatic advance and retreat is probably attributable to "an eustatic rise and fall of sea level" during Cambrian-Ordovician time; and they called for further testing of the hypothesis. This hypothesis can lead to some reinterpretations of the Grand Canyon Cambrian strata, and future research bears intent tracking.

DEVONIAN. The Grand Canyon Devonian, represented by the mostly Frasnian (early Late Devonian) Temple Butte Limestone, is not well studied (McKee, 1969, 1974). In the eastern Grand Canyon, the Temple Butte occurs only as intermittent deposits filling channels in the top of the Muav Limestone; in the western Grand Canyon it is a thicker, laterally continuous unit. The first record of the Temple Butte was by Walcott (1880) who noted in the then-unnamed formation only the presence of armored fishes; he did not mention

invertebrates until 1883 when he reported only that the unit contained "... Cyathophylloid corals, casts of Brachiopods and Gasteropods, and plates of Placogonoid fishes ..." (Walcott, 1883, p. 438). Later surveys of the Grand Canyon Paleozoic section briefly addressed the Devonian rocks, generally remarking on the fragmentary fish remains rather than on any invertebrates. Walcott (1890a) applied the name "Temple Butte" to the discontinuous channel deposits of eastern Grand Canyon, but the Temple Butte was not formally recognized by that name in the western Grand Canyon until McKee (1937a, 1938b, 1939), in progress reports of field reconnaissances in the Canyon's Paleozoic strata, correlated the formation westward.

Fossils in the Temple Butte are both poorly preserved and poorly represented in the channel-fill sediments of the eastern Grand Canyon. Beus (1969), on the basis of stratigraphic similarity, tentatively correlated the eastern Temple Butte with the Frasnian Jerome Member of the Martin Formation of north-central Arizona, where fossils are much more abundant. Possibly transported conodonts were noted by Beus (1969) in the Jerome Member. Recognizing that these fossils would be useful in correlating other Devonian sections in northwestern Arizona, where diagnostic macrofossils are absent, Beus indicated that continued investigations of the conodont fauna were in order. Later, Beus (1980, p. 62) reported:

"Recently a few conodonts were recovered from the Temple Butte at Matkatamiba Canyon . . . which suggest a latest Givetian to late Frasnian age (Dietmar Schumacher, personal communication, 1978). Forms identified by Schumacher include: 1) *Polygnathus pennatus*, *P. xylus*, and *Icriodus* cf. *I. subterminous*--possibly a late Givetian lowermost *Polygnathus asymmetricus* Zone assemblage, 2) *Pandorinellina insita* and '*Spathagnathodus*' cf. '*S. gradatus*'--possibly an early Frasnian assemblage, and 3) *Polygnathus* cf. *P. angustidiscus*, probably an early late Frasnian form."

From west of the Grand Canyon, Beus (1980, p. 62) reported "Rare silicified corals, crinoid plates, gastropods, and massive stromatoporoid colonies" in the Temple Butte at Iceberg Ridge. [Beus has brought to my attention a 1983 M.S. thesis by Scott Ritter of Brigham Young University; but I have not had the opportunity to see this thesis. Ritter reported Famennian conodonts at the top of the Devonian sequence at Iceberg Ridge; he called this 25-m interval a "Crystal Pass" equivalent.]

Beus (1980) interpreted the paleoenvironments and paleogeography of the northern Arizona Devonian. He saw in the eastern Grand Canyon during Frasnian time "an intertidal deposit that formed on an elongate platform (here called the Grand Canyon shelf), the surface of which was generally

just above or just below high tide level." This shelf was in turn "surrounded by a shallow sea with open circulation to the south and west, where a normal marine fauna occurred . . . , but restricted circulation to the east . . ." (Beus, 1980, p. 68). Beus also was of the opinion that the Temple Butte of western Grand Canyon "correlates with the Muddy Peak Limestone in Nevada and probably should be recognized by that name in northwestern Arizona, outside of Grand Canyon" (p. 64). He remarked, too, that the supra-Muav undifferentiated dolomites of the western Grand Canyon could be ?Cambrian-?Devonian in age, although no diagnostic fossils had been found.

MISSISSIPPIAN. The Mississippian System is dramatically represented in the Grand Canyon by the 500-ft-high cliff of the Redwall Limestone and by recently discovered buried-valley deposits of Chesterian (Late Mississippian) age in the top of the Redwall in western Grand Canyon. (The Chesterian deposits will be discussed in a separate subsection.)

The geologic history of the Redwall Limestone is exhaustively presented in McKee & Gutschick's (1969) already classic monograph. That monograph also includes paleontological chapters by Betty Skipp (foraminifera), William J. Sando (corals), Helen Duncan (bryozoans), Ellis L. Yochelson (gastropods and pelecypods), W. M. Furnish (cephalopods), Donald B. Macurda, Jr. (blastoids), and James C. Brower (crinoids). McKee and Gutschick jointly authored a chapter on "Algae and Stromatolites, Holothurians, Trilobites, Ostracodes, and Fish" and a short note on an incompletely studied collection of brachiopods.

Fossils have been recognized in the Redwall Limestone by all of the early investigators in this region. However, the first principally paleontological work on the Redwall Limestone was on the coral faunas (Gutschick & Easton, 1942, abstract) outside of the Grand Canyon. This study was later expanded and formally published (Easton & Gutschick, 1953), and four species (three new) in four genera were identified from the Grand Canyon. The stratigraphic distributions of the coral species were graphically plotted, but in a generalized stratigraphic column representative of the Redwall near Jerome, Arizona.

It remained for McKee (1960b) to apply his principles of key-bed correlation to the Redwall Limestone. In subdividing the Redwall into four distinct members (formally named by McKee, 1963), he was able to trace lithologic and paleontologic zones great distances through northern Arizona, identifying the progression of facies of the Redwall sea. McKee (1960a) also demonstrated that the Redwall is a cyclic deposit, an interpretation which influenced later paleoecological and paleogeographical reconstructions.

With research underway toward what would be McKee & Gutschick's (1969) Redwall monograph, several byproducts were generated by associate

investigators. Yochelson (1962) published descriptions of some gastropods from the Redwall. Sando (1963) published a new species of colonial rugose coral, supported by specimens including a paratype from Grand Canyon localities. But neither of these works dealt with the new stratigraphic findings by McKee. Coral zones of the Redwall were first delineated by Sando (1964); only the *Dorlodotia inconstans* Zone is represented in the Grand Canyon, from Pakoon eastward nearly to Havasu Canyon. This zone is, however, particularly interesting because it straddles the boundary between the Mooney Falls and Horseshoe Mesa Members (a boundary established on bedding criteria). The zone's absence to the south, in the Mogollon Rim region of north-central Arizona, was an indication to McKee that the Horseshoe Mesa Member had been removed in that area by post-Redwall erosion. Skipp (in Skipp *et al.*, 1966) identified nine species and subspecies of foraminifera (four new taxa) in four genera, and one questionable genus to which specific determinations were not made.

The most obvious of paleontological observations in McKee & Gutschick's (1969) monograph is the little variance in age determinations between localities, as interpreted from faunal groups. Aided by such good correlation, Skipp (1969) arbitrarily delineated six endothyrid foraminiferal zones in the Redwall; in ascending order they are: *Septaglomospiranella* Assemblage Zone (Kinderhookian age), *Tuberendothyra paratumula* Assemblage Zone (Osagian), *T. tuberculata* Assemblage Zone (Osagian), *Endothyra spinosa* Assemblage Zone (Osagian), *Eomillerella* [*Eoendothyranopsis*, cf. Skipp & McKee (1978)] *spiroides* Range Zone (Osagian-Meramecian; this range zone is recorded only in the Grand Canyon), and *E. scitula* Range Zone (Meramecian). Brachiopods and some coral genera also occur in distinct zones in the Redwall, a distribution that is eminently applicable to stratigraphic correlation and paleoecological interpretations of facies (McKee & Gutschick, 1969, p. 128):

"[Zonation] is further illustrated by the relatively large number of genera and species of various animal groups, which has no apparent relation to the number of individuals, in successive members of the formation. Vertical distribution of organisms also largely reflects the distribution of facies, as illustrated by many groups that are common wherever certain rock types occur but that are rare or absent elsewhere."

The Redwall brachiopod collection mentioned by McKee & Gutschick (1969, pp. 435-437) is composed of nearly 2,000 specimens: more than 50 species in at least 30 genera, dominantly *Spirifer*, "especially those of the type that in the past commonly have been referred to as *S. centro-natus*." They represent a variety of zones and wide geographic distribution. The preliminary

study of this collection had been undertaken by J. T. Dutro, Jr., but had not been completed "due to unforeseen circumstances." Although plans had been made to publish the brachiopod study as a supplement to the Redwall monograph, the collection remains incompletely studied (E. D. McKee, written commun., 1982).

Supplementary discoveries and research on the Grand Canyon Mississippian have been made since McKee & Gutschick's monograph was published. In 1966, a group of travelers on the Colorado River bypassed a normal stopping point at Redwall Cavern, in Marble Canyon, and instead pulled out at Mile 34.8,* where it was warmer. One member of the party found an exposure of fossils in a small side canyon which, upon subsequent examination, proved to be specimens of *Rayonnoceras* sp., an orthocone nautiloid [Rayonnoceras Croneis, 1926]. They were found in the top three feet of the Whitmore Wash Member of the Redwall Limestone, and the canyon in which they were found was later informally named Nautiloid Canyon. This was the first record of this genus from the Redwall, and the first orthocone nautiloid from the Grand Canyon (Breed, 1969; Billingsley & Breed, 1976). One well exposed specimen, thought by Breed (1969) to show impressions of soft parts, was later shown to actually be the shell etched and weathered in such a manner as to give the appearance of tentacle impressions (Billingsley & Breed, 1976).

In 1968, George Billingsley supplemented the Nautiloid Canyon *Rayonnoceras* specimens by finding better exposed specimens in the identical stratum in Kanab Canyon. In 1974, he discovered at Mile 34.3, at river's edge (low-water) on the west bank, a poorly preserved coiled nautiloid; this also in the Whitmore Wash Member. Other new nautiloid localities are scattered between Fossil Canyon (Mile 124.8; the largest specimens known, measuring 36 in. long and 6-1/2 in. in diameter) and Whitmore Canyon (Mile 188.6). On the whole, though, nautiloids are rare in the Redwall Limestone (Billingsley & Breed, 1976).

CHESTERIAN (LATE MISSISSIPPIAN). At the top of the Redwall Limestone, sediments of Chesterian age have been dated by paleontologic criteria. The Chesterian beds were first mentioned by McKee & Gutschick (1969, p. 74) from a 6.5-ft-thick limestone unit capping the Redwall at Bright Angel Trail. The fauna contained in that unit is limited to "abundant brachiopods and some foraminifers."

Until 1979, the Bright Angel locality was the only known Chesterian deposit in the Grand Canyon region; but in that year buried valleys in the western Grand Canyon were discovered by Billingsley and confirmed by McKee (U.S. Geological Sur-

vey, 1979). Age determinations were made paleontologically by M. Gordon, Jr. (marine invertebrates), B. Skipp (foraminifera), and R. B. Kosanke (plants). These buried valleys, occurring in the upper surface of the Redwall Limestone, below the basal conglomerate of the Watahomigi Formation, have been interpreted by Billingsley & McKee (1982) to be part of an extensive drainage system that had developed when the area was uplifted, ending deposition of the Redwall sediments. The valleys, averaging 1,000 ft wide and 280 ft deep (maximum known depth of the valleys is 401 ft), were cut into the upper Redwall sediments and by the close of Chesterian time had been completely filled with marine and continental sediments.

Billingsley & McKee (1982) subdivided the Chesterian sediments of the buried valleys into "lower" (terrestrial) and "middle" and "upper" (marine) units. The "lower unit" contains plant fragments and palynomorphs (addressed in the section on Paleozoic floras). The "middle unit" fauna is represented by a collection of 187 invertebrate megafossils. M. Gordon, Jr. (in a written communication cited by Billingsley & McKee) identified one coral specimen, 11 brachiopods, 10 molluscs, some remains of blastoids and crinoids, one trilobite, and a shark dentition. The most common form is a brachiopod identified by Gordon as a small *Inflatia* near *I. clydensis* (Girty) [*Inflatia* Muir-Wood & Cooper, 1960]. W. J. Sando (written communication cited by Billingsley & McKee), from a zone of poorly preserved corals in the "middle unit" at Granite Park, identified *Michelinia* sp. and *Barytichisma* sp., neither of which is diagnostic of stratigraphic age. From this same zone, Betty Skipp identified in thin sections "abundant bryozoan and pelmatozoan debris, and lesser amounts of ostracode, trilobite, and brachiopod detritus," together with an alga, *Asphaltina* sp., and a tubular calcareous foraminifer, *Pseudoglomospiranella* sp. (Billingsley & McKee, 1982, pp. 143-144).

The "upper unit" fauna, examined by Gordon, contains a limited variety and quantity of marine invertebrate species. Gordon stated, however, that "these species 'are not as definitive' as those in the lower limestone [i.e., "middle unit"]" (Billingsley & McKee, 1982, p. 144). Skipp identified in the "upper unit" seven foraminiferal genera and an alga, *Ortonella* sp.

In the buried-valley deposits, the eosigmoilinid foraminifera are important indicators of the Chesterian age of the unit. These are *Eosigmoilina explicata* Ganelina and "*E.*" *rugosa* Brazhnikova (= *Quasiarchaediscus* of Mamet) (Billingsley & McKee, 1982, citing a 1978 written communication from Skipp).

PENNSYLVANIAN-PERMIAN SUPAI GROUP. McKee (1975) subdivided the Supai formation, raising the Supai to group rank. The lower three formations of the Supai Group are, in ascending order, the Watahomigi, Manakacha, and Wescogame Forma-

*By convention, distances downstream along the Colorado River are measured in miles, with Mile 0 at Lees Ferry, Arizona. The Grand Wash Cliffs, at the mouth of the Grand Canyon, are at Mile 278.

tions, which are Pennsylvanian in age. McKee also raised the upper Supai's Permian Esplanade Sandstone member to formation rank; it is the uppermost of the four Supai formations. The previous stratigraphic nomenclature and age assignments of these strata are confusing, but they are succinctly set straight by McKee (1982, Table A1). As McKee (1982, p. 5) pointed out:

"The Supai and its correlatives in northwestern Grand Canyon and adjoining parts of Arizona, Nevada, and Utah did not receive much attention until the early 1950's when McNair (1951) proposed two new formations and reorganized the local stratigraphy. One of these formations, the Pakoon Limestone, is considered (in this report) to be a western equivalent of the lower part of the Esplanade Sandstone. For this reason and because much of the fossil evidence dating the upper part of the Supai comes from the Pakoon Limestone, it is included [in this report] . . . even though not part of the Supai Group"

This stratigraphic relationship is also adopted in the present paper. The reader should refer to McKee (1982, pp. 3-5) for a concise and authoritative historical review of previous research on the Supai Group.

Fauna of the Supai Group include marine invertebrates, ichnites of vertebrates, and some land plants. (The ichnites and land plants will be elaborated upon in later sections of this paper.) McKee (1982, p. 77) summarized the marine fauna:

"Each of the four formations comprising the Supai Group in Grand Canyon locally contains a faunal assemblage represented by numerous individuals, but relatively few genera and (or) species. Of the 11 animal groups included, the brachiopods have the greatest variety with a total of 27 genera and (or) species. Next in order of abundance (number of genera and (or) species) are pelecypods with 23, gastropods with 20, and corals with 11. Among the megafossils the brachiopods are the most common form from the standpoint of individuals and are most widespread.

"The distribution and concentration of individuals within each formation clearly seem to have been controlled by environmental factors that reflect geographic position and age.
* * *

Other marine fauna of the Supai include trilobites, bryozoans, crinoids, echinoids, conodonts, conulariids, algae, foraminifera, and fusulinids. The microfauna, however, are problematical in the Supai because they are most

often found in sediments deposited under high-energy conditions; transportation and abrasion of some specimens is quite evident. Much fossil material appears in the Supai as bioclastic debris. Reworking of underlying formations, with transferral of some organisms to the younger formation, has complicated the dating of these formations.

McKee (1982, pp. 75-112) and Gordon (1982) have so competently and exhaustively outlined the distribution of fossils in the Supai Group that a comprehensive summary cannot be conveniently presented within the limited space of this paper. Instead, short abstracts of the principal components, features, and interpretations of the Supai assemblages are presented in the following paragraphs, based mostly on McKee's and Gordon's findings.

Gordon (1982, Table F1) presented a locality table for the whole Watahomigi megafauna that includes numerous references to fossil groups containing indeterminant genera and species, and to probably new genera and new species. Gordon has stated that the Watahomigi Formation is quantitatively and taxonomically the most fossiliferous formation of the Supai Group, with "more than 85 species of megafossils" having been recognized therein. The Watahomigi marine fauna is concentrated in three zones within the formation, the most prominent groups being productid and spiriferid brachiopods, mostly *Composita* cf. *C. gibbosa*.

The Manakacha Formation is sparsely fossiliferous. Only six groups of megafossils--all from western Grand Canyon--have been reported from this formation. These include three brachiopod genera, two of bryozoans, two of pelecypods, and one genus each of gastropod, trilobite, and coral. The most common fossil is probably a large species of *Bellerophon*, but the most diagnostic are the fusulinids (five genera indicating an Atokan age for the formation). B. Mamet (in a 1972 written communication to McKee, cited in McKee, 1982) recognized 13 genera of small foraminifera that can be assigned to specific microfacies but are not time-restricted.

In the Wescogame Formation, fossils again are not common, but, due in part to the high-energy environment of deposition, they are geographically widely distributed. Brachiopods and bryozoans are not found, and the most common fossils are at least six genera of pelecypods. Large bellerophons also are noted. None of these groups, however, occur in the higher-energy deposits; they favored the more quiet environments. The presence of the fusulinid *Triticites* sp. and corals *Syringopora multattenuata* McChesney, *Canina* sp., and *Ozawainella*? sp. support the Virgilian age assigned to this formation. The distribution of nonfusulinid foraminifera is in similar microfacies rather than by age. These similar microfacies are found throughout the Supai Group; they contain 14 nonfusulinid species, including four of endothyrids.

The Esplanade Sandstone is almost completely free of fossils; only a meagre ichnofauna and a few plant remains are mentionable, and the highly cross-stratified sandstones contain some nondescript bioclasts. In the western Grand Canyon, however, the highly fossiliferous Pakoon Limestone intertongues with the Esplanade. The Pakoon fauna is composed mostly of corals (nine genera), fusulinids (six genera), and smaller foraminifera (at least six genera), with lesser numbers of brachiopods (four genera), gastropods (four genera), and fragmentary echinoderms. One locality yielded an unidentified bryozoan, and sharks teeth were found at two other places. The coral material was said by W. J. Sando (quoted by McKee, 1982, p. 89, from a 1964 written communication) to "show affinities to the Lower Permian faunas * * * from the Ely area, Nevada" [ellipsis McKee's]. The presence of the small foraminifera *Geinitzina*? sp., *Spandelinoides*? sp., and *Calci-vertella* sp. near the base of the Pakoon have pointed to an Early Permian age. The fusulinids *Schwagerina* and *Pseudoschwagerina*, however, are diagnostically Wolfcampian in age. But as for the Esplanade Sandstone, McKee (1982, p. 89) stated: "As yet no fusulinids have been found in the Esplanade to establish whether or not it is precisely equivalent in age to the Pakoon; apparently the cross-bedded sand represents an environment unfavorable to marine life."

Overall, the most important of the Supai fossils are the fusulinids and brachiopods that provide determinant ages for various units in the Group. Although some units are sparsely or completely free of fossils, enough material has been collected during the past 20 years to establish different time boundaries within the Supai. On fossil evidence correlated through the Canyon and to nearby areas, the Watahomigi is Morrowan in age in its lower two-thirds and probably Atokan in age in its upper third. The Manakacha Formation is composed almost completely of Atokan-age sediments. However, the fusulinid *Eoschubertella* sp., found in the western Grand Canyon, is apparently an Atokan-Des Moinesian fossil that has been considered by some workers to belong only in the Des Moinesian. No definite diagnostically Des Moinesian fusulinids have been found in the Grand Canyon although they occur in rocks to the south and west of the Canyon. At the top of the Manakacha there is an unconformity that might represent Des Moinesian and Missourian times. The Wescogame is Virgilian in age, established by the probably-Virgilian fusulinids *Triticites* spp. found near the base of the formation and by other Late Pennsylvanian fusulinids and corals higher in the section. The Esplanade Sandstone, completely devoid of diagnostic fossils, fortunately intertongues in its lower part with the Pakoon Limestone which is demonstrably Wolfcampian in age. But the age of the upper Esplanade, which to the west rests on top of the Pakoon, is uncertainly Wolfcampian. McKee (1982, p. 111) remarked: "An early Leonardian age has been suggested for it by Walter Pierce (written commun., 1976) on the basis of a fusulinid that he collected

from the upper part of the Pakoon at Grand Gulch. The specimen was identified as *Schwagerina linearis* and interpreted as 'Upper Wolfcampian' by George J. Verville." However, if this "Upper Wolfcampian" fusulinid is an accurate diagnosis, one must bear in mind its stratigraphic proximity to the Leonardian Hermit Shale.

PERMIAN HERMIT SHALE, COCONINO SANDSTONE, TOROWEAP FORMATION, AND KAIBAB LIMESTONE. Of all of the Grand Canyon strata, the Permian ones have received the most attention from geologists. This no doubt is partly attributable to the widespread distribution and relative ease of access to Permian localities in northern Arizona and adjoining areas. First discussions of the Permian strata of the Grand Canyon region were made by Blake (1856) and Marcou (1858), although the Permian of the Grand Canyon-proper was not mentioned until Newberry (1861) published his "Geological Report." In terms of stratigraphic Stage names, this sequence of rocks is now known to be simply Wolfcampian to Leonardian in age, but the stratigraphic relationships and ages of these units were matters of frequent reassignment for a half century (see McKee, 1938a; 1969; 1982, Table A1).

Hermit Shale. Fossils of the Hermit Shale are mostly a remarkable Early Permian flora and some interesting vertebrate ichnites; these will be discussed in separate sections of this paper. But the Hermit also has yielded the Grand Canyon's entire collection of fossil insects: four specimens. Two specimens represented new species of the same genus: *Tupus gilmorei* Carpenter, 1927, and *T. whitei* Carpenter, 1928. *T. gilmorei* was found in 1926 by C. W. Gilmore during his studies of the ichnofauna along Hermit Trail. The first record of this fossil was by Sturdevant (1926b):

"One of the slabs collected, containing plant remains, was found upon examination at the National Museum to contain also the well-preserved wing of a large dragon-fly-like insect. According to Dr. Gilmore, 'This wing is over four inches in length and well enough preserved to be identified when once I get around to study it.'" Sturdevant concluded, "... this unique discovery of the first fossil insect in this part of the country will undoubtedly prove to be a considerable scientific value."

Although Sturdevant was too optimistic about the significance of the then-unique find, the few Grand Canyon fossil insects are nonetheless interesting.

When Carpenter (1927) described *T. gilmorei* he remarked that it is not taxonomically critical to the understanding of the Meganeuridae (to which taxonomic family *Tupus* Sellards, 1906, belongs), but it is of interest in reconfirming the age of the Hermit Shale because *Tupus* is restricted to the Early Permian. Before *T. gilmorei* was described, *Tupus* was known only by the genotype, *T. permianus* Sellards, from the Early Permian of

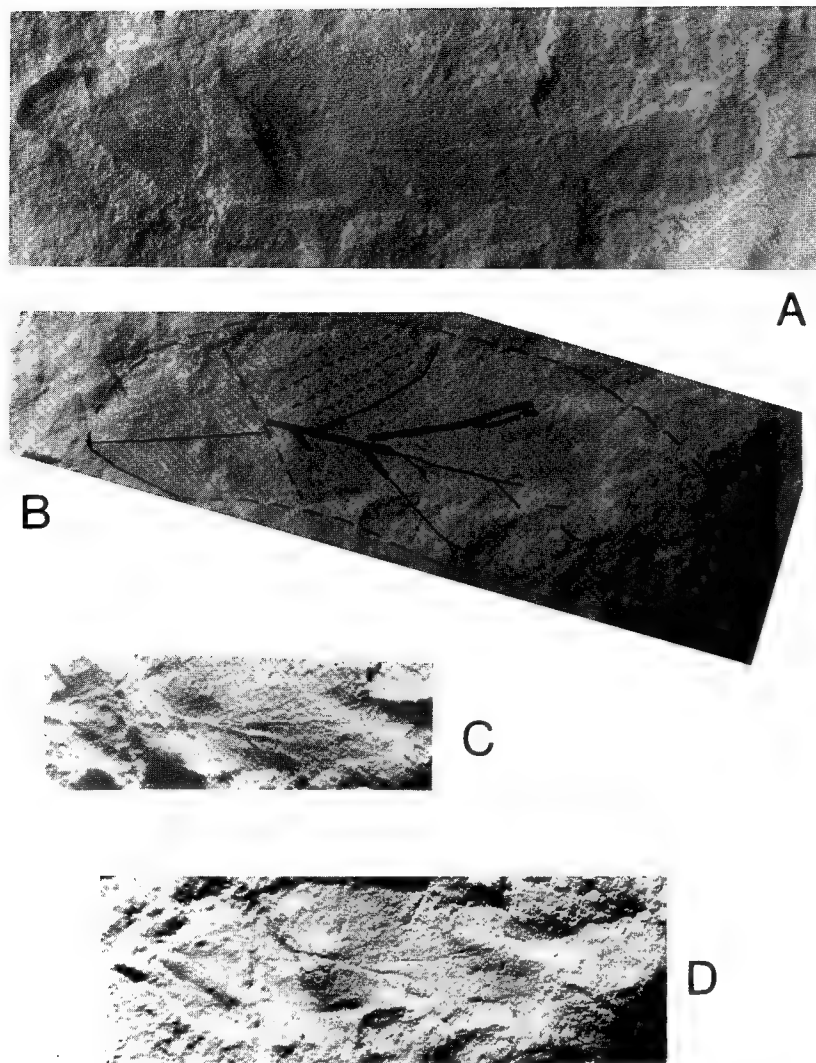


Figure 6. Poorly preserved "blattid forewing" from the Early Permian Hermit Shale, Bright Angel Trail (USNM 71712). This is the third known Grand Canyon insect specimen, heretofore unfigured and undescribed, collected by David White in 1927 and identified without discussion by Carpenter (1928). All photographs show the specimen in the same angle of orientation. **A:** General view of the specimen, illuminated from the lower right to better show the line of taphonomic breakage(?); X 2.4. The apparent outline of the specimen is illusory because most of its periphery is covered by matrix. **B:** General view of the specimen, illuminated from the upper left; X 2.4. Superimposed on the photograph is a diagram that illustrates definite venation (bold lines) and apparent venation (light lines) visible by inspection of the specimen. Dashed line transecting the proximal end of the specimen delineates the line of taphonomic breakage(?). Parallel lines of short dashes mark the area that exhibits parallel lineation. Solid lines along the outline show what appear to be actual edges of the specimen. The dashed parts of the outline approximate the form of the wing, assuming that the solid lines show true edges; this is done for illustrative purposes only, and no morphologic implications are made. **C, D:** Higher-contrast views showing some of the venation; both X 1.8. **C** shows the proximal and central parts of the wing, illuminated from the lower right. **D** shows approximately the same area as **A**, illuminated from the upper left.

Kansas. (*Tupus* is a member of the Order Protodonata. The known range of this extinct Order of predaceous insects is from the Late Carboniferous to the Permian; cf. Tasch, 1973.)

In 1928, Carpenter described *Tupus whitei* from a specimen collected by David White along Bright Angel Trail. Carpenter (1928, p. 186) also reported, without further remark, the only other fossil insect specimens found in the Grand Canyon: "... these specimens are so incompletely preserved that their exact affinities cannot be determined; one appears to be the posterior half of an Odonate insect, and the other, a forewing of a blattid." All of David White's Grand Canyon material is in the U.S. National Museum (USNM), but the presumed odonate was apparently never catalogued and cannot now be located (F. J. Collier, written commun., 1981). This is most unfortunate because the Order Odonata (dragonflies) is known to have first appeared in the Early Permian (cf. Tasch, 1973), so this specimen would be among the earliest known odonates. The blattid forewing, however, is in the USNM collections, and in 1981 I briefly examined this specimen.

It has never been referred to in the literature since Carpenter's (1928) brief mention, probably because it is so poorly preserved that even its taxonomic family has not been determined; hence, it cannot be named.

The unique specimens *Tupus gilmorei*, *T. whitei*, and the blattid forewing comprise the entire existing collection of Grand Canyon fossil insects. The heretofore undescribed blattid deserves an informal description, at least, for the sake of historical completeness:

Order Blattodea

Family, Genus, and Species Indeterminant

(Figs. 6A-D)

"forewing of a blattid." Carpenter, 1928, *Psyche*, 35: 186.

Specimen: USNM 71712 [Label with specimen reads, "Blattid fam.?"]

Description: The specimen appears to be a complete forewing, but its periphery is apparently covered by matrix. Venation is well defined only in the middle of the specimen. There is a prominent vein approximately following the central axis of the wing. An

unconnected secondary vein just above the center probably connects with the prominent vein, but direct visible evidence is lacking.

Apparent traces of venation are observed under low-power magnification. In addition, very faint parallel lineations are seen in one section of the wing, but whether these are trace venation or are diagenetic markings could not be ascertained by this cursory examination.

The proximal portion of the wing may have suffered taphonomic breakage, or creasing with folding, prior to consolidation of the sediment. This break occurs clearly and angularly across the proximal portion of the wing. The prominent vein abruptly terminates at this line; a faint central line, offset from but possibly continuing the prominent vein, extends to the proximal extremity of the wing.

It should be pointed out that the specimen also resembles a neuropterid plant. It was identified as a blattid by Carpenter, an authority on paleoentomology; and it seems unlikely that its collector, David White, an authority on paleobotany, would have not recognized it as a plant. But the specimen is from a formation noted for its plant material, and the venation of the neuropterids and blattids are similar. These observations, taken together with the poor preservation of the specimen, Carpenter's cursory description of it, and its having been completely ignored by later researchers, provide sufficient reason to question any classification. Furthermore, the specimen has not been prepared for closer examination by removing the obscuring matrix around its edges, if indeed the periphery has been preserved.

Matrix: The specimen is very poorly preserved in a red, fine- to medium-grained sandy shale containing occasional 1-mm grains of white quartz sand. The grain size of the matrix has prohibited preservation of the characteristic fine venation required for taxonomic classification.

Occurrence: Hermit Shale (Early Permian), Bright Angel Trail, Grand Canyon National Park, Arizona. Collected by David White, June, 1927.

Coconino Sandstone. The Coconino Sandstone contains only an ichnofauna of vertebrates and invertebrates of a desert-dune environment. This will be discussed in the section on the ichnofauna.

Toroweap Formation and Kaibab Limestone. Finally, the uppermost formations of the Grand Canyon are the late Early Permian Toroweap Formation and Kaibab Limestone. As mentioned, these units were first examined in the Grand Canyon region as early as the 1850s. From the Canyon proper, Newberry made the first collection of Grand Canyon fossils--brachiopods and echinoids, most of them new species (Newberry, 1861). Although some early publications indicate that Newberry's collections are at Columbia University (e.g., Jackson, 1912, pp. 261, 267-268), they are in fact in the U.S. National Museum (F. J. Collier, written commun., 1982; see also Spamer, 1984, p. 92). McKee (1938a, p. 157) has determined that Newberry's fossils were probably collected from the Toroweap Formation. (See also McKee's 1938 monograph for an historical review of early studies of the Grand Canyon Permian strata.)

Walcott (1880) presented the results of the first detailed stratigraphic survey of the Permian strata in the Grand Canyon, observed during his inaugural expedition down Kanab Canyon. The

Kaibab and Toroweap Formations constituted Walcott's "Upper Aubrey [*sic*] group," in which he identified 34 fossil species in 23 genera of pelecypods and gastropods. He stated (p. 224), "The Permian character of the fauna, taken with the evidence afforded by the stratigraphy, clearly establishes the Permian as a well-defined and distinct group in the Colorado Valley." (The Aubrey Group, a term recommended for abandonment by McKee [1982, p. 31] was introduced by Gilbert [1875] for the whole stratigraphic sequence from the Kaibab Limestone down to and including the Manakacha Formation [*cf.* McKee, 1982].)

Not until 1910, however, did the higher Permian strata of the Grand Canyon undergo any sort of nomenclatural revision. Darton (1910) divided the Upper Aubrey group of Dutton (1882) into the Kaibab limestone and Coconino sandstone. (Darton's Kaibab was equivalent to all of Walcott's [1880] Upper Aubrey, and the Coconino was equivalent to the upper part of Walcott's Lower Aubrey.) McKee (1938a) completed the division in use today, subdividing Darton's Kaibab into the Kaibab Limestone and Toroweap Formation. However, it was Noble's (1914, 1922, 1928) and Reeside & Bassler's (1922) work that indicated that the Canyon's higher Permian strata were divisible into smaller units. These researches, partly on the evidence of fossils, contributed to the correlation of strata through and beyond the Grand Canyon.

As already mentioned in the subsection on the Tonto Group, E. D. McKee is responsible for developing the analytical principle of key beds. This principle and the stratigraphic concepts behind it evolved during his reconnaissances of the Grand Canyon's Paleozoic section (*cf.* McKee, 1937a,b; 1938a,b; 1939; 1940), although there is some evidence to indicate that the key-bed concept was recognized somewhat earlier (*cf.* McKee, 1934b, 1935d): McKee (1934b) published a short note on a remarkable 3- to 4-ft-thick fossiliferous limestone bed in the middle Kaibab (*i.e.*, near the top of the alpha member of the Toroweap Formation) that can be traced a great distance through the Grand Canyon. (Even more astounding than the continuity of the bed is the extreme abundance in it of the pelecypod *Schizodus*. McKee (1934b) noted: "With over a hundred individuals included in a block of one cubic foot, it is apparent that in the thirty or more miles over which their remains are scattered, they must occur by the millions or even billions." However, as McKee [1938a] pointed out, pelecypods are present in every fossiliferous facies of the Kaibab and Toroweap; so this particular record is most significant as a record of one of the earliest identifications of a key bed in the Grand Canyon.)

McKee's monograph on the Kaibab and Toroweap unveiled the value of tracing key sedimentary and faunal beds over great distances and elaborated upon distinctions between vertical and lateral changes in lithology and faunal composition. In

what before had been a laterally monotonous "Kaibab limestone," McKee defined two formations, each with three informal members composed of laterally distinct facies. The members in each formation are called, in descending order, "alpha," "beta," and "gamma" members. The Kaibab alpha and beta members each contain five facies, and the "western phase" of the Toroweap alpha and beta each contain two facies; the respective gamma members are single-facies units. The Toroweap also contains "transition" and "eastern" phases in which unfossiliferous cross-bedded sandstones intertongue with the red beds, gypsum, and chemical limestones of the western phase. Not all facies are represented at the Grand Canyon-proper, and not all contain fossils.

In summary, the Kaibab-Toroweap fauna is composed of brachiopods, corals, bryozoans, crinoids, and pelecypods in an open-sea facies, and most molluscs, scaphopods, trilobites, and cephalopods in restricted saline- and brackish-water facies. The brachiopod fauna is sufficiently important that McKee (1938a) discussed it separately, describing 24 species (four new, and one new subspecies) in 15 genera, and two identifications only to genus.

Although the principles of facies analysis and key-bed correlation are not as clear-cut in the Kaibab-Toroweap as they are in the Tonto Group, the geographic distribution and accessibility of the Permian formations has permitted the construction of a much more complete three-dimensional picture of transgressive-regressive sequences.

Subsequent to McKee's authoritative monograph, research on the Grand Canyon Permian strata included continued contributions on the paleofauna and biostratigraphy of these units, although most of these works dealt with much larger geographic areas or stratigraphic intervals. Faunal works include those on nautiloids or ammonoids (Miller & Unklesbay, 1942; Miller & Youngquist, 1949; Miller & Furnish, 1958), trilobites (Snow, 1945; Cisne, 1971), and sponges (Finks, 1960; Griffin, 1966). Wholly or partly biostratigraphic reviews and interpretations include those of Bissell (1962), Fisher & Sorauf (1962), McKee & Breed (1969), Baars (1979), Rawson & Turner-Peterson (1980), and Clark (1981). McKee & Breed (1969) provided a comprehensive review of paleontological studies in the Kaibab-Toroweap from the time of McKee's 1938 monograph to 1969.

Most recently, a needed contribution to the study of the Kaibab Limestone bryozoans in the Grand Canyon was presented by McKinney (1983). He reported three species (one new) in three genera and additional specimens identified only to five genera. Previous work on the Grand Canyon Permian bryozoans is sparse. McKee (1938a, pp. 157-158) briefly mentioned bryozoans, including an unpublished study of these fossils wherein David Keppel had identified six genera and some new species among 30 specimens from the

eastern Grand Canyon. Moore & Dudley (1944, p. 304) described a new species from the Kaibab Plateau. Condra & Elias (1945a) named a new genus and species, "*Bicorbula*" *arizonica*, from the Grand Canyon, but later (1945b) they renamed the genus *Bicorbis* after learning that the genus was preoccupied by *Bicorbula* Fisher, 1887. The initial paper (1945a) also included a list of associated fossils, including other bryozoans.

Miscellaneous items of interest on the Kaibab-Toroweap fauna of the Grand Canyon are some fossil shells preserving original colors and a problematical coelenterate. McKee (1930b) noted in two specimens of the brachiopod *Chonetes* "a beautiful pale pink color," although he was unsure (but fairly convinced) that the colors represented original colors. Four years later, McKee (1934b) added to these specimens a pelecypod, *Schizodus*, with a "pale blue" color. He remarked that these long-extinct specimens with original colors add "a touch of reality to the ancient Permian sea and its fauna." Still later, McKee (1947b) included the *Chonetes* specimens (for the first time specifically identified as *C. subiliratus*, from the Kaibab Limestone) and the *Schizodus* sp. specimen (from the Toroweap Formation) in a general paper on original colors in fossil shells. At that time he supplemented the Grand Canyon collection with six more specimens from the Kaibab Limestone, all of the brachiopod *Derbyia nasuta* Girty, each with "a large, spectacular shell of greyish or brownish old rose color" (McKee, 1947b, p. 48). He also observed that the colors of the Kaibab and Toroweap specimens are uniform over the whole shell, which he interpreted as an indicator of primary, not secondary, coloration.

The holotype of the scyphozoan *Conularia kaibabensis* McKee, from the Kaibab Limestone, was the first specimen of this genus to have been reported from the Arizona Permian (McKee, 1935a). The problematical genus *Conularia* Miller in Sowerby, 1821 (cf. Sinclair, 1952; Sinclair & Richardson, 1954), was for some time erroneously applied to the Gastropoda but now is considered to belong to the Coelenterata (cf. Moore & Harrington, 1956). McKee (1935a) did not remark on any previous identifications of his *C. kaibabensis*, but when I asked him for some information on a "fossil fish" noted in the Grand Canyon literature (Anonymous, 1926), he replied that he was "quite certain" that the description therein refers to his *Conularia* (McKee, written commun., 1982). (The 1926 note describes the specimen as ". . . an imprint of the ribs and backbone of a fish . . ." and gives credit to A. L. Brown for its discovery near Bright Angel Point on the North Rim.) McKee (1935a) credited Charles Merriam for a 1928 discovery, but McKee had come across the specimen after it had been deposited in the museum collections on the South Rim. McKee (written commun.) recalled "distinctly" that for a while after its discovery, rangers and local residents insisted the fossil was that of a fish. In light of McKee's certainty that the

1926 note refers to his *Conularia*, I suggest that the record of discovery should be emended to Brown, 1926.

Paleozoic Vertebrates

Paleozoic vertebrate fossils are not common in the Grand Canyon. Their rarity in proportion to other kinds of fossils is more a function of taphonomic loss than of true disproportionality in the contemporary environment. This disparity is especially evident in the Supai Group and Coconino Sandstone, wherein vertebrate ichnites are abundant but fossil vertebrate parts are rare; in fact, vertebrate parts are unknown in the Coconino. Were it not for the fortune of proper conditions for preservation of the ichnites, the vertebrate paleofauna of these formations would be virtually unknown. (The ichnofossils will be discussed in a later section.)

DEVONIAN. Walcott (1880) made the first notes on vertebrate fossils in the Grand Canyon. In a brief description of the then-unnamed Temple Butte Limestone, he noted "the presence of Placoganoïd fishes of a Devonian type" (Walcott, 1880, p. 225). More than 40 years passed before a report of new Grand Canyon Devonian fossils was published, when Noble (1922) mentioned his collection of scales and plates. He had submitted these fossils to J. W. Gidley for examination, who determined that only the armored placoderm *Bothriolepis* Eichwald, 1840, was represented in the collection and who observed that the genus was particularly characteristic of the Late Devonian. Gidley, in correspondence with Noble (Noble, 1922, p. 52), wrote that the specimens were "too fragmentary to be determined specifically" although they did resemble *B. nitidens* from the Devonian of New York. Schuchert (1918a, p. 361) stated that in 1916 Noble had informed him of Gidley's determinations. Noble indicated at that time that at "Sapphire Canyon he found an abundance of fish remains that have been identified . . . as scales of *Holoptychius* and plates of *Bothriolepis* nearest to *B. nitidens* . . ." [*Holoptychius* Agassiz in Murchison, 1839]. Noble (1922) did not mention *Holoptychius*, so that identification may by then have been retracted. However, Denison (1951) cited and accepted Schuchert's observation of *Holoptychius*. Noble's Sapphire Canyon locality was located in 1930 by a party of National Park Service naturalists who looked for additional fish specimens; but they found only "very fragmentary parts" (McKee, 1930a).

Denison (1951) called *Bothriolepis* a diagnostic Late Devonian fresh-water fish, an observation that apparently verifies the inferred depositional environment of the Temple Butte channel deposits of eastern Grand Canyon. He recognized only two species of this genus in the western United States, *B. coloradensis* Eastman and the new species *B. darbiensis* Denison, the former being the species recognized in the Temple Butte Limestone of the Grand Canyon. About this Deni-

son (1951, p. 230) remarked: "The [Grand Canyon] remains are not sufficiently well preserved to permit specific identification, but the reticular, non-tubercular type of ornamentation on plates of rather large size suggests that they may belong to *B. coloradensis*."

McKee (in Poole *et al.*, 1967, p. 903) noted that Frasnian (early Late Devonian) channel deposits of northwestern Arizona "locally contain abundant plates of the brackish- or fresh-water fish *Bothriolepis* sp.," but no discussion was published either on Denison's remarks or the paleoecological significance of these and invertebrate fossils in the sediments.

MISSISSIPPIAN. From the Redwall Limestone, McKee & Gutschick (1969) noted the presence of six genera of fishes (not listed by McKee & Gutschick). Nearly all were represented only by teeth, and specific identifications were not possible. These authors said that none of the genera are particularly useful in diagnosing the depositional environment because they have been found in sediments that represent different environments.

The Chesterian channel deposits of the western Grand Canyon (described earlier) have to date yielded only shark teeth (Billingsley & McKee, 1982).

PENNSYLVANIAN. In the Watahomigi Formation, a few fish fragments have been found. Gordon's (1982, pp. 119, 121) biostratigraphic study of the Watahomigi notes one spine of "*Deltodus* sp., *mercurii* Newberry" and three dentitions of *Deltodus* sp. (as identified by D. H. Dunkle), all from different localities [*Deltodus* Morris & Roberts, 1862; *D. mercurii* Newberry, 1876].

PERMIAN. Where the Pakoon Limestone intertongues with the lower Esplanade Sandstone, shark teeth have been reported from the Pakoon. Dunkle has identified *Cladodus* Agassiz, 1843, and *Deltodus* from collections made at Iceberg Canyon (McKee, 1982, p. 94).

A tooth of *Deltodus mercurii* was collected by McKee from the beta member of the Kaibab Limestone, a discovery that extended upward the known stratigraphic range of this shark, to the late Early Permian (McKee, 1938a).

The most interesting of the Grand Canyon vertebrates is probably the giant petalodontid shark *Megactenopetalus kaibabianus* David. It was described in 1944 as a new genus and species based on a then-unique incomplete (right half) multicusped dentition found in the beta member of the Kaibab Limestone near Point Sublime (North Rim). This shark is remarkable for the great difference in size between it and presumably related late Paleozoic fishes. Other petalodontid dentitions are mostly less than an inch in width, but the reconstructed holotype of *M. kaibabianus* contains some of the largest such teeth known: the dentition exceeds 5 in. (David, 1944; Ossian, 1976). *Megactenopetalus* remains a monospecific

genus, represented by only eight known specimens (M. Hansen, 1978).

Despite the rarity of *M. kaibabanus*, it has been reported from around the world: Arizona (three specimens), New Mexico (one), Texas (one), Iran (one), and the Peoples Republic of China (two). Ossian (1976) made the first significant contribution toward the understanding of this unusual shark by publishing a redescription of *M. kaibabanus* and supplementing the holotype with three additional specimens from Arizona, New Mexico, and Texas. (The Arizona specimen came from the alpha member of the Kaibab Limestone, near the type locality.) In 1978, M. Hansen described the third Arizona specimen, the only known lower dentition of *M. kaibabanus*. The specimen, re-discovered in the collections of the U.S. National Museum, is an incomplete tooth and incomplete spine found in the Permian Concha Limestone of Santa Cruz County, Arizona. M. Hansen (1978, p. 55) remarked that "The associated spine, presumably belonging to *M. kaibabanus*, is a rare occurrence of an ichthyodorulite in apparent organic association with a petalodontiform dental element." The incomplete (left half) lower dentition has let us see this shark as a predator that scooped up prey with its single-cusped lower dentition (reconstructed by M. Hansen, 1978, to measure 4.4 in. wide and 2.2 in. high). The shark, closing its jaws, could simultaneously stab and hold with the multicusped upper dentition and vertically slice with the sharp single-edged cutting blade of the lower. Yet despite the efficiency of such a formidable mouth, *M. kaibabanus* was one of the last of the petalodonts, surviving only from Leonardian time (late Early Permian) to Dzhulfian time (closing Permian) (M. Hansen, 1978). Ossian (1976, p. 395) hypothesized that a few groups of shark-like fishes like *Megactenopetalus* may have "trended toward giantism before extinction overtook them in the lower Mesozoic."

M. kaibabanus is the only petalodont known from the southwestern United States. Ossian (1976, p. 395) suggested that its occurrence there "may represent an attempt by this taxon [the petalodonts] to colonize new areas in response to a period of stress." Paleolatitudinal distributions of *M. kaibabanus* indicate that it was restricted to equatorial waters. The American specimens occurred near the Permian equator, the Iranian specimen (cf. Golanshi & Janvier, 1974; *vide* Ossian, 1976, and M. Hansen, 1978) came from near 20° S., and the Chinese specimens (*Petalodus shingkuoi* Young, 1950, and *P. cf. shingkuoi* of Liu & Hsieh, 1965; declared by M. Hansen, 1978, to be synonyms of *M. kaibabanus*) from near 15° N. (M. Hansen, 1978). [The references for Young, 1950, and Liu & Hsieh, 1965, are cited in the list of references of the present paper because of some problems encountered with the citations in my original sources.]

Paleozoic Trace Fossils*

Trace fossils are found throughout the Grand Canyon Paleozoic strata. The Cambrian Bright Angel Shale, however, is by far the richest source of trace fossils of any unit in the Grand Canyon.

The first trace fossils to be found in the Canyon were two species of *Cruziana* d'Orbigny, 1842, probably from the Bright Angel Shale. The two species, *C. linmarssoni* and *C. rustica*, were first described by C. A. White in 1874 and more fully described and figured by him in 1877. White considered his new fossils to be plants, classifying them under "Cryptogamia, Class Thallogenes." (*Cruziana*, together with related forms, has been the subject of much discussion for more than a century. Some early workers thought *Cruziana* was a fossil plant or sponge, while others proposed an inorganic origin. Osgood [1970, 1975] has summarized this controversial history.)

In 1918, Walcott presented a study of the tracks and trails of trilobites. In the study, he included *Cruziana* in this general grouping of fossils, essentially regarding generic distinctions to be useful only as classifications of form. Walcott figured several Grand Canyon specimens, including the unnamed specimen that White (1877, p. 49) described as a "series of minute tracks that were probably made by some small Crustacean or other Articulate."

C. W. Gilmore, who made the only comprehensive study of the Grand Canyon ichnofaunas, took note of a few trails in the Cambrian Tapeats Sandstone (Gilmore, 1928b). In noting Walcott's (1918) discussion of Tapeats trails, Gilmore indicated that his collection supplemented Walcott's by describing some new characteristics of these trace fossils. McKee (1932a; and in McKee & Resser, 1945) also sustained Walcott's interpretations of these traces as having been made by trilobites. (For conclusions on studies of *Cruziana* specifically, see Seilacher, 1962. *Cruziana*, with related forms together referred to as the *Cruziana* ichnofacies, is now used as a bathymetric zonation indicator for the area of well-sorted sands and silts of deeper shallow waters; cf. Seilacher, 1964, 1967.)

Another problematical trace fossil from the Middle Cambrian of the Grand Canyon is *Eophyton*

*In this paper, ichnofossils are divided into two groups based on zoologic affinity. This is done for convenience and no taxonomic significance is implied. The term "trace fossil" is used for those fossils preserved as tunnels, borings, and a variety of traces and trails made by invertebrates that generally left no distinct trail of "footprints;" this group includes worms, jellyfishes, trilobites, and the like. The terms "ichnite" and "ichnofauna" are reserved for the special fauna of footprints and trackways found in the Supai Group, Hermit Shale, and Coconino Sandstone; these are the footprints and trackways of vertebrate and invertebrate legged animals, specifically quadrupeds and such arthropods as arachnids or scorpionids.

Torell, 1868. The genus has been variously described as a plant, a trace fossil made by invertebrates, or an inorganic sedimentary feature. Häntzschel (1975, p. W173), although listing *Eophyton* with the pseudofossils, noted that the marking was "produced by organisms or inorganic objects," and he referred the reader to Kieslinger (1939) for a short description of various interpretations. Walcott (1898, p. 63) considered his figured specimens of Grand Canyon *Eophyton* (probably from the Tapeats Sandstone) to be the trace fossils of medusae trailing their tentacles across mud. (Walcott also said that a trail on the same slab with one of the *Eophyton*, shown in his pl. 38, had been made by a trilobite.)

Wanless (1981) has mentioned in an abstract that the Bright Angel Shale contains "Organism structures, tadpole ripples, and rare mud cracks" which indicate shallow-water depositional environments. Trace fossils of many kinds are, in fact, common in the Grand Canyon's Cambrian strata. In some instances they have served paleobiological studies by indirectly indicating the presence of abundant life in the contemporary sediments, in the absence of determinant fossils. For example, Schuchert (1918b, p. 369) remarked that in the Muav Limestone he had "not seen a Paleozoic marine deposit more bored into and consumed by mud eaters than this one" McKee (1938a, p. 107) identified this stratum as the Gateway Canyon Member, stating that Schuchert had been led to making that remark by the abundance of "Worm borings and fucoid-like casts [that] are common in the thin-bedded limestones"

"Fucoids," or worm-like ridges, are found throughout the Grand Canyon stratigraphic column because the term is a catch-all category. The name stems from the Fucaceae, whose wormy, interwoven appearance can be so conveniently compared to many true and pseudofossils. Fucoids of any sort are usually not particularly useful in interpreting paleoenvironments but are nonetheless interesting. McKee (1932a) presented a brief synopsis of some of the Grand Canyon fucoids; this work, though, is the only such summary available. He recorded fucoids from the late Precambrian Dox Formation; these he said were possibly organic, but more probably represent remnants of dried mud or mineral crystal impressions like those of ice. From green shales of the Tonto Group, fucoids collected by Walcott and attributed by him to annelid worm trails and trilobite burrows were said by McKee to be confirmed by a newer collection from the Tapeats Sandstone. From the Muav Limestone, McKee noted abundant fucoids, but he said that they were of inconclusive origin. Fucoids from the Coconino Sandstone were interpreted as coprolites (and in his 1933 survey of the Coconino Sandstone McKee again alluded to the coprolitic fucoids). Last, McKee noted in sandy phases of the Kaibab Limestone (the as yet unsegregated Kaibab-Toroweap Formations) fucoids which he interpreted as seaweeds.

In 1955, Seilacher made a collection of trace and pseudofossils in the late Precambrian and Cambrian strata of the Grand Canyon. He included descriptions and analyses of these and previously published fossils within a comprehensive survey of Cambrian ichnofossils (Seilacher, 1956). From the Grand Canyon Cambrian strata Seilacher reported an unspecified trilobite track and five trace fossil genera as follows (classifications in parentheses are adopted from Häntzschel, 1975; comparisons within brackets are those of Seilacher, 1956): cf. *Bergaueria* Prantl, 1946 (probable coelenterate resting burrow) [described by McKee & Resser (1945, pl. 8, fig. d) as "natural casts of small circular depressions"]; *Corophioides* Smith, 1893 (U-shaped spreiten burrow) [described by McKee & Resser (1945) as "probable worm borings" (pl. 7, fig. b) and "fucoid-like structures" (pl. 9, fig. c)]; *Teichichnus* Seilacher, 1955 (endogenic burrow of unknown producer) ["probable worm borings" of McKee & Resser (1945, pl. 6)]; cf. *Scolicia* de Quatrefages, 1849 (gastropod trail) ["circular trails" of McKee & Resser (1945, pl. 5, fig. a)]; and *Phycodes* Richter, 1850 (morphologically variable features), specifically *P. pedum* Seilacher and "*Phycodes* n.sp.". Seilacher (written commun., 1983) now considers the undescribed "new species" to be "a 'feather-stitch' modification of *Phycodes pedum*," about which he also said, "I have found similar forms in the Cambrian of Sweden, but to my knowledge, nobody has later taken up this taxonomic problem." (Osgood, 1970, thought that *P. pedum* should be placed under a separate new genus.)

David White (1929a) included in his monograph on the Early Permian flora of the Hermit Shale two new genera and species of trace fossils, *Scoyenia gracilis* and *Walpia hermitensis*, which he placed under "Vermes?". White (1929a, p. 115) described *S. gracilis* as "Slender rope-like remains, probably molds." *Scoyenia* White is, according to Müller (1969; *fide* Häntzschel, 1975, p. W106), "probably made by [the] same animal (polychaete worm?) or one similar to that making [the] ichnogenus *Tambia* Müller." *Scoyenia* is an index trace fossil for the *Scoyenia* ichnofacies of bathymetric zonation (*cf.* Seilacher, 1967), which is characterized by nonmarine, mostly red bed sediments. *Walpia*, described by White (1929a, p. 117) as "Irregularly winding molds, varying slightly in diameter," is listed by Häntzschel (1975, p. W120) as "?Made by worms or crustaceans," a pronouncement which is unchanged from White's interpretation.

Specimens of *Walpia hermitensis* were reported by White (1929a) only from the lower Hermit Shale along Hermit Trail, while *Scoyenia gracilis* occurred in the Hermit Shale along Hermit and South Kaibab Trails. McKee (1982, p. 100) has noted "wormlike tubes" of *S. gracilis* in association with the alga *Rivularites* in the Esplanade Sandstone and in the Watahomigi and Manakacha Formations.

A new ichnogenus and species of oligochete(?) worm, *Scolecocoprurus cameronensis*, was described

by Brady (1947) from the Coconino Sandstone. Its occurrence is in the canyon of the Little Colorado River, about six miles below Cameron, or about 20 miles east of the Grand Canyon. The close geographic position of the type locality to the Grand Canyon makes the type specimen a candidate for inclusion in my catalogue of Grand Canyon type fossils (see Spamer, 1983, 1984). A few types from Lees Ferry, the Kaibab Plateau, and Anita are already in the catalogue, so this close locality has precedents among localities not in the Canyon-proper. This is the 190th taxon in the catalogue, but a formal Grand Canyon Type Fossil Number will not be assigned until it appears in a future supplement to the catalogue. (*Scolecocoprus* has since been noted in the Permian Kaibab Limestone, too, as mentioned in the next paragraph.)

From the beta member of the Kaibab Limestone, Decourten (1980) has identified the ichnogenera *Palaeophycus* Hall, 1847 (widely different forms) [descriptions in parentheses adopted from Häntzschel (1975)], *Planolites* Nicholson, 1873 (burrows infilled with material having passed through the gut of a worm, difficult to distinguish from *Palaeophycus*), *Cosmorhaphis*? Fuchs, 1895 (grazing trail) [not noted by Häntzschel (1975) to occur in Arizona; and it is apparently without record of any Permian occurrences, although Häntzschel listed its known range as ?Ordovician to middle Tertiary], and *Scolecocoprus* Brady, 1947 (as a "stuffed burrow" nearly synonymous with *Taenidium* Heer, 1877 [see Häntzschel (1975, p. W112, not p. W102 as listed in index)]), as well as "*Cruziana*-like forms" and "pellet-lined tubes." The latter two ichnogenera and the *Cruziana*-like forms are, according to Decourten, especially interesting because they are found only in facies composed mostly of clastic materials laid down in a high-energy environment. From studies of these fossils and the substrates in which they are found, feeding behaviors, preservation potential, and facies influence on the distribution and character of the ichnofauna can be determined. This Decourten stressed could be important in reconstructing paleoenvironments "within the broad shallow marine framework," an area of paleontological study that has not been vigorously studied.

Generally speaking, trace fossils can be found throughout the Grand Canyon Paleozoic strata. They are the usual trails, tunnels, and borings by invertebrate animals. But some trace fossils have been detected in rock units that previously had been thought to be barren of fossils. Apparently structureless sandstones of the Permian Esplanade Sandstone are demonstrably stratified; in some selected samples, X-ray analysis shows "the weak traces of dipping foreset planes and the cross-cutting tunnels or borings of wormlike animals . . ." (McKee, 1982, p. 241).

Ichnofauna of the Supai Group, Hermit Shale, and Coconino Sandstone (Pennsylvanian to Permian)

FIRST STUDIES. C. D. Walcott was credited by Gilmore (1928b) for having collected the first fossil footprints from Grand Canyon strata. The specimen, Gilmore noted, was found by Walcott in 1903 in the Coconino Sandstone along Grandview Trail; the find antedated by 12 years Charles Schuchert's discovery of Grand Canyon ichnites near Hermit Trail. For some reason Walcott never described or mentioned the Grandview Trail trackway. Walcott's specimen, identified by Gilmore (1928b) as the invertebrate ichnotaxon *Ootopodichnus didactylus* Gilmore, was rediscovered by Gilmore in the U.S. National Museum collections. Although the Grandview specimen supplemented the holotype of *O. didactylus*, described one year earlier from the Hermit Trail locality (cf. Gilmore, 1927b), Gilmore (1928b) suggested that the Grandview specimen might represent a distinct species if better-preserved material could be found. He also noted that the Grandview Trail locality was a new one for ichnites.

Schuchert (1918a) mentioned having found ichnites in the late Paleozoic strata, and it was this collection that Lull (1918) used in the first published description of Grand Canyon ichnites. Lull identified four species (all new) in three genera (one new). The tracks of the new genus and species of quadrupeds, *Laoporus schucherti* and *L. noblei*, found in the Coconino Sandstone, were at once noted by Schuchert and by Lull to have been preserved on the foresets of dunes, always advancing upslope. This apparently peculiar trait would in later years become the subject of much study. From the Supai Group, Lull remarked on two new species--perhaps of undescribed genera--that he named *Megapezia coloradensis* and *Exocampe delicatula*. He thought that these ichnites most closely resembled the amphibian ichnogenera *Megapezia* from the Early Carboniferous of Nova Scotia and *Exocampe* from the Triassic of Connecticut.

In 1924, C. W. Gilmore was invited by the National Park Service to visit Schuchert's Coconino ichnite locality, to make a collection for the U.S. National Museum and to prepare an *in situ* exhibit of tracks along Hermit Trail. (At that time, Hermit Trail was used by tourists visiting Hermit Camp operated by the Santa Fe Railroad near Hermit Creek. The trail is now abandoned and the camp no longer exists.) Gilmore (1926a,c) reported that both objectives had been accomplished and that the known variety of Coconino ichnites had been expanded to at least eight genera and ten species. The tracks of invertebrates were recognized in these rocks for the first time, and the collection as a whole was thought to be Carboniferous in aspect. The collection was formally described by Gilmore (1926b), in which report he recorded nine species (seven new) in nine genera (four new) of vertebrate ichnites and two new genera and new species of in-

vertebrate ichnites.

Gilmore (1926b) also discussed a series of track-like markings found in the Supai Group of Fossil Bay. Citing information passed along by S. Hubbard, Gilmore noted that the markings, thought by local Havasupai Indians to be the tracks of horses, bore a "striking resemblance" to the doubtful ichnospecies *Hoplichnus equus* Hitchcock from the Triassic of Connecticut. But Gilmore (1926b, p. 38) concluded that the Supai occurrence was not fossil--"nothing more than a staining of the sandstone"--and went on to propose (p. 39), "May it not be that the Supai markings are stains resulting from the decay of some gelatinous medusa-like animals that were stranded on a sandy beach?" McKee (1982, pp. 95-96), however, has reported similarly formed and sized impressions in the Esplanade Sandstone in Hidden Canyon: "No information is available on the type of animal represented, but the pairing of the impressions, the common directions of orientation, and the uniformity of shape, all suggest an origin as trackways of a quadrupedal animal" (p. 96).

The Marsh Fund Committee of the National Academy of Sciences supported a second Grand Canyon ichnite expedition in 1926 (Gilmore, 1927a). This time, Gilmore returned to the Coconino locality but expanded his collecting range to the Hermit Shale and Supai Group along both Hermit and Yaki (South Kaibab) Trails.

"The expedition was successful far beyond expectations," Gilmore (1927a, p. 45) wrote. "Fossil tracks were found in considerable abundance in all three of these formations and at several levels in the Hermit Trail section.... This later investigation shows that in the perfection of their preservation and in the great variety of footmarks found, there are few localities that outrank this one."

In his second formal report, Gilmore (1927b) described from the Coconino Sandstone 17 species (seven new) in 10 genera (one new) of vertebrate ichnites and five species (three new) in five genera (two new) of invertebrate ichnites; from the Hermit Shale, eight species (five new) in seven genera (one new) of vertebrates; and, from the Supai Group, three new genera and species of vertebrate tracks. He included in that report a list of all known North American Carboniferous ichnites (60 species in 34 genera), noting that they were "badly in need of revision, a task that would doubtless decrease rather than increase the totals given" (p. 10). In spite of Gilmore's own prolific neology among the Grand Canyon ichnotaxa, his proclamation not only would be proven true by later research but remains a valid and timely remark.

A third Grand Canyon ichnite-collecting expedition was funded by the Grand Canyon Exhibit Committee of the National Academy of Sciences; Gilmore led this expedition in 1927. More specimens were collected for the U.S. National Museum;

and more *in situ* exhibits were prepared, this time in the Coconino Sandstone and the Supai Group along South Kaibab Trail within sight of what is now called the Yavapai Museum (Gilmore, 1928a). This final expedition yielded still more new genera and species which Gilmore (1928b) described in a third formal report. In that report he discussed five species (two new) in five genera (one new) of vertebrate ichnites and some unnamed invertebrate trails. He also announced (p. 3, footnote) the discovery of the first North Rim ichnite localities (see also Gilmore & Sturdevant, 1928).

Gilmore's Grand Canyon ichnites became widely known soon after the first expedition (e.g., *New York Times*, 1926; Merriam, 1926) and were called upon thereafter to help illustrate to the general public the wonders of fossils and the Grand Canyon (e.g., Merriam, 1930). The Grand Canyon ichnofauna became scientifically recognized, too, although largely ignored afterward because most of the new ichnospecies, and even most of the new ichnogenera, are apparently unique to the Grand Canyon.

White (1929a, p. 118) also briefly described a poorly preserved impression that he listed as *Hastimima?* sp. (referred to *Hastimima* White, 1908). The figure caption (White, 1929a, p. 220, pl. 51, fig. 1) calls the specimen a "Problematical fossil, regarded as the impression of the thick leathery integument of an animal, possibly a crustacean related to the Euripterid [*sic*] *Hastimima*." The collection locality of this Hermit Shale specimen was not specified by White, and the fossil has never again been referred to in the Grand Canyon literature.

QUESTIONS IN NOMENCLATURE. Most of the Grand Canyon ichnofaunal nomenclature remains valid by reason on non-study. In 1947, Brady published a significant contribution toward understanding some of Gilmore's Grand Canyon ichnogenera. With specific reference, first, to Gilmore's (1927b) *Unisulcus sinuosus*, Brady referred the species to his new ichnogenus *Diplopodichnus*. [In ignorance of Brady (1947), I listed Gilmore's *U. sinuosus* as "*Gordia sinuosa* (Gilmore)" in my catalogue of Grand Canyon type fossils (Spamer, 1983, p. 442; 1984, p. 119): based on Häntzschel's (1962) listing of *Unisulcus* Hitchcock, 1858, as a junior synonym of *Gordia* Emmons, 1844, I moved *U. sinuosus* to *Gordia* with obviously too enthusiastic confidence. I here emend the catalogue to acknowledge Brady's formal reassignment of *U. sinuosus* to *Diplopodichnus* Brady.]

Although neither the genotype *Diplopodichnus biformis* Brady nor Brady's (1947) two other new ichnogenera ("*Isopodichnus*" and *Scolecocoprus*) are known to be represented by specimens from the Grand Canyon, their occurrence in the Coconino Sandstone of northern Arizona suggests that they could still be found in the Canyon. [Brady (1949) named the substitute ichnogenus *Oniscoidichnus* to replace *Isopodichnus* which was preoccupied by *Isopodichnus* Bornemann, 1889, and he

declared that these two isopod taxa are not congeneric.] *Diplopodichnus* and *Oniscoidichnus* (as "*Isopodichnus*") were referred by Brady (1947) to the Diploda and Isopoda, respectively, but both with question; *Scolecocoprus* was referred to the Annelida (discussed in the section on Paleozoic trace fossils).

Brady (1947) also named the new species *Octopodichnus minor*, from north of Seligman, Arizona. This is the second known species of this scorpionid(?) ichnogenus, the genotype *O. didactylus* Gilmore having been found in the Grand Canyon.

The second and last taxonomic contribution from Brady on the Grand Canyon ichnogenera was his note describing the new species *Palaeoheloura* [sic, nom. null.] *dunbari* Brady, 1961. Its occurrence is in the Coconino and DeChelly Sandstones of northern Arizona, but it is not known to occur in the Coconino at the Grand Canyon. Like Brady's other northern Arizona ichnotaxa, though, *P. dunbari* could yet be found in the Canyon.

The fossil taxa of the Coconino Sandstone that supplement the Grand Canyon ichnofauna, specimens of which might be found at the Canyon by future workers, are:

Diplopodichnus Brady, 1947

D. biformis Brady, 1947, genotype, from north of Seligman

Octopodichnus Gilmore, 1927

O. minor Brady, 1947, from north of Seligman

Oniscoidichnus Brady, 1949

O. feliciformis (Brady), 1947, genotype, from north of Seligman

Paleoheloura Gilmore, 1926

P. dunbari Brady, 1961, from north of Ash Fork

As for reviewing or revising all of the ichnotaxa from the Grand Canyon, little has been accomplished. Aside from a few modifications by Gilmore, and Brady's reassignment of "*U.*" *sinuosus*, Baird (1952; 1965; and in Breed, 1967) has presented the only taxonomic revisions pertaining to Grand Canyon ichnotaxa. In 1952, he revised the labyrinthodont amphibian ichnogenera *Limmopus*, *Allopus*, and *Baropus* Marsh: he reassigned *Allopus? arizonae* Gilmore to *Baropezia* Matthew, and he declared *Baropus coconinoensis* Gilmore, 1927, to be synonymous with *Baropezia eakini* Gilmore, 1926. (*Limmopus? coloradensis* Henderson, 1924, from Colorado, was transferred by Gilmore [1926b] to *Laoporus* Lull and was thought by him to be possibly synonymous with *Laoporus schucherti* Lull, 1918, from the Grand Canyon; but Baird [1952] commented only on the generic reassignment.) In 1965, Baird synonymized the vertebrate ichnotaxon *Ammobatrachus turbatus* Gilmore, 1928, with *Tridentichnus supaiensis* Gilmore, 1927, in the process vacating the genus *Ammobatrachus* Gilmore. In a personal communication quoted by Breed (1967), Baird made *Dromilopus parvus* Gilmore, 1927, syn-

onymous with *Batrachichnus delicatulus* (Lull), 1918, thereby vacating *Dromilopus* Gilmore, too. Breed's (1967) article recorded the discovery of a trackway in Supai-type sediments inside Stanton's Cave in Marble Canyon (easternmost Grand Canyon). Although the trackway was insufficiently preserved to identify positively, Baird noted that it was nonetheless indistinguishable from *B. delicatulus* of the Hermit Shale. That a Hermit-type trackway was found in Supai sediments is academic, according to Baird: "the footprint fauna of the Supai is very incompletely known, and trackmakers of this type undoubtedly lived in Supai time" (quoted by Breed, 1967, p. 70).

In the early 1950s, Baird had assembled molds of most of Lull's and Gilmore's trackways, intending to completely redescribe and zoologically interpret that material. "But," Baird has said (written commun., 1982), "it soon became evident that the taxonomy couldn't be treated without a wholesale restudy of published Paleozoic footprint taxa in order to determine what few of the published names are definable and establish (obviously lengthy) synonymies." He collected casts of most of the North American material but was unable to acquire some of the European taxa necessary to carry out the study. Unfortunately, this study of such grand proportions remains incomplete, and we are left with most of Lull's and Gilmore's original ichnotaxa, although they probably are not wholly valid. Table 4 lists the present status of the Grand Canyon ichnotaxa.

From preliminary studies, though, Baird has made some observations (written commun., 1982, 1983) that bear repeating. Their inclusion here alerts the research community that nomenclatural and taxonomic questions exist:

1) "The Supai-Hermit assemblages are . . . largely assignable to previously-described Pennsylvanian genera" (1982).

2) ". . . '*Dolichopodus*' is simply *Laoporus*" at a running gait, ". . . and the trackmaker was neither an amphibian nor a lacertoid but probably a caseid pelycosaur" (1982, 1983).

3) "*Nanopus merriami* Gilmore is removed from *Nanopus* and assigned with confidence to *Laoporus*; the species is retained provisionally because of its stratigraphic position some 120 feet below the level of *L. schucherti* and *L. noblei*" (1983).

4) "*Nanopus maximus* is transferred to *Barypodus* as a presumably valid ichnospecies. *Barypodus metzseri*, which I suspect was based on a trackway made by the same individual, becomes a junior synonym by page priority." But since page priority is no longer mandatory, "a better option would be to make '*N.*' *maximus* a junior synonym of *B. metzseri*," this because the removal of both "*N.*" *merriami* [see No. 3] and "*N.*" *maximus* altogether eliminates *Nanopus* from the list of known Grand Canyon ichnotaxa (1983).

Table 4. Current Status of Grand Canyon Pennsylvanian-Permian Ichnofauna of the Supai Group, Hermit Shale, and Coconino Sandstone¹

| Current Status ² | Grand Canyon Type Fossil No. ³ | Previous Nomenclature or Junior Synonyms; Remarks and Sources |
|-------------------------------------|---|--|
| Invertebrates | | |
| <i>Diplopodichnus</i> Brady, 1947 | | |
| <i>D. sinuosus</i> (Gilmore), 1927 | 118 | <i>Unisulcus sinuosus</i> Gilmore; applied to <i>Diplopodichnus</i> Brady (1947, pp. 469-470) |
| <i>Mesichnium</i> Gilmore, 1926 | | |
| <i>M. benjamini</i> Gilmore, 1926 | 119 | Genotype by original monotypy |
| <i>Ootopodichnus</i> Gilmore, 1927 | | |
| <i>O. didactylus</i> Gilmore, 1927 | 120 | Genotype by original monotypy |
| <i>Paleoheloura</i> Gilmore, 1926 | | |
| <i>P. tridactyla</i> Gilmore, 1926 | 121 | Genotype by original monotypy |
| <i>Triavestigia</i> Gilmore, 1927 | | |
| <i>T. niningeri</i> Gilmore, 1927 | 123 | Genotype by original monotypy |
| Invertebrate trail, no. 1 | -- | Gilmore (1928, pp. 10-12) |
| Invertebrate trail, no. 2 | -- | Gilmore (1928, p. 12) |
| Vertebrates | | |
| <i>Agostopus</i> Gilmore, 1926 | | |
| <i>A. matheri</i> Gilmore, 1926 | 125 | Genotype by original monotypy |
| <i>A. medius</i> Gilmore, 1927 | 126 | |
| <i>Amblyopus</i> Gilmore, 1926 | | |
| <i>A. pachypodus</i> Gilmore, 1926 | 128 | Genotype by original monotypy |
| <i>Anomalopus</i> Gilmore, 1927 | | |
| <i>A. sturdevanti</i> Gilmore, 1927 | 130 | Genotype by original monotypy |
| <i>Baropezia</i> Matthew, 1903 | | |
| <i>B. arizonae</i> (Gilmore), 1926 | 127 | <i>Allopus?</i> <i>arizonae</i> Gilmore; transferred provisionally by Baird (1952) |
| <i>B. eakini</i> Gilmore, 1926 | 131 | = <i>Baropus coconinoensis</i> Gilmore, 1927 (Grand Canyon Type Fossil No. 132); Baird (1952) |
| <i>Barypodus</i> Gilmore, 1926 | | |
| <i>B. palmatus</i> Gilmore, 1926 | 133 | Genotype by original monotypy |
| <i>B. metszeri</i> Gilmore, 1927 | 134 | = <i>Nanopus maximus</i> Gilmore, 1927 (Grand Canyon Type Fossil No. 146); cf. Baird (written commun., 1983), this paper |
| <i>B. tridactylus</i> Gilmore, 1927 | 135 | |

Table 4 (cont'd)

| | | |
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| <i>Batrachichnus</i> Woodworth, 1900 | | |
| <i>B. delicatulus</i> (Lull), 1918 | 136 | <i>Exocampe? delicatula</i> Lull (Gilmore, 1927) = <i>Dromilopus parvus</i> Gilmore, 1927 (Grand Canyon Type Fossil No. 140); Baird, cf. Breed (1967). <i>Dromilopus</i> Gilmore, 1927, vacated |
| <i>B. obscurus</i> Gilmore, 1927 | 137 | |
| " <i>Collettosaurus</i> " Cox, 1874 | | <i>Nomen dubium</i> , cf. Baird (written commun., 1983), this paper |
| " <i>C.</i> " <i>pentadactylus</i> Gilmore, 1927 | 138 | <i>Nomen inquirendum</i> |
| <i>Cursipes</i> Matthew, 1903 | | |
| <i>C. sp.</i> | -- | Cf. Gilmore (1927) |
| <i>Hylodichnus</i> Gilmore, 1927 | | |
| <i>H. bifurcatus</i> Gilmore, 1927 | 141 | Genotype by original monotypy |
| <i>H. whitei</i> Gilmore, 1928 | 142 | |
| <i>Laoporus</i> Lull, 1918 | | |
| <i>L. schucherti</i> Lull, 1918 | 144 | Designated the genotype; possible synonym is <i>L. coloradensis</i> (Henderson), 1924 (Gilmore, 1926) |
| <i>L. coloradensis</i> (Henderson), 1924 | -- | Cf. Gilmore (1926) |
| <i>L. merriami</i> (Gilmore), 1926 | 147 | <i>Nanopus merriami</i> Gilmore; cf. Baird (written commun., 1982), this paper |
| <i>L. noblei</i> Lull, 1918 | 145 | |
| <i>L. tetradactylus</i> (Gilmore), 1926 | 139 | <i>Dolichopodus tetradactylus</i> Gilmore; cf. Baird (written commun., 1982), this paper. If sustained, <i>Dolichopodus</i> Gilmore, 1926, vacated |
| <i>Palaeopus</i> Gilmore, 1926 | | |
| <i>P. regularis</i> Gilmore, 1926 | 148 | Genotype by original monotypy |
| <i>Palaeosauropus</i> Hay, 1902 | | |
| <i>P. hermitanus</i> (Gilmore), 1927 | 143 | <i>Hylopus hermitanus</i> Gilmore; cf. Baird (written commun., 1983), this paper |
| <i>Parabaropus</i> Gilmore, 1927 | | |
| <i>P. coloradensis</i> (Lull), 1918 | 149 | Genotype <i>Megapezia? coloradensis</i> Lull, by original monotypy |
| <i>Stenichnus</i> Gilmore, 1927 | | |
| <i>S. yakiensis</i> Gilmore, 1927 | 150 | Genotype by original monotypy |
| <i>Tridentichnus</i> Gilmore, 1927 | | |
| <i>T. supaiensis</i> Gilmore, 1927 | 151 | Genotype by original monotypy = <i>Ammobatrachus turbatans</i> Gilmore, 1928 (Grand Canyon Type Fossil No. 129); Baird in Lewis & Vaughn (1965); <i>Ammobatrachus</i> Gilmore, 1928, vacated |

(cont'd)

Table 4 (cont'd)

Incertae Sedis

| | | |
|---------------------------------|----|--|
| <i>Incertae sedis</i> , no. 1 | -- | Gilmore (1927, pp. 64-65) |
| <i>Incertae sedis</i> , no. 2 | -- | Gilmore (1927, p. 65) |
| Like <i>Hoplichnus equus</i> | -- | "Pseudo-track-like markings" of Gilmore (1926, pp. 37-39); McKee (1982, p. 96) |
| Miscellaneous indefinite tracks | -- | Gilmore (1928, pp. 12-13) |

¹Including written communications cited by Breed (1967) and this paper.

²Gilmore (1926, 1927, 1928) = Gilmore (1926b, 1927b, 1928b) of references cited in this paper.

³Cf. Spamer (1983, 1984).

Zoologic Affinity, Paleoenvironments, and Stratigraphic Distribution

Baird (1965, p. C49) pointed out several problems in the study of ichnofaunas, including the ichnites of the Grand Canyon formations. He wrote: "The classic ichnofaunas from North American red beds--those of the Supai and Hermit Formations in the Grand Canyon . . . and the Clear Fork Group at Castle Peak, Tex. . . --were gravely misunderstood by their describers and need extensive redescription and taxonomic revision before they can be compared fruitfully with contemporary footprints and skeletal material." Such study is still awaited. Other complications are encountered in "tracing Permian footprint genera back into the Pennsylvanian" and in comparisons of the North American material with the somewhat better understood Permian ichnofaunas of central Europe and Great Britain.

Environment not only dictated the types of animals that could be supported under those conditions, it played a crucial role in the mode of footprint creation and methods of preservation. Ichnofaunas therefore represent not only the paleofauna, but the physical characteristics and taphonomic processes of the paleoenvironment. As Baird (1965, p. C49) observed, ichnofaunas of Permian beach and dune sands are remarkably different from those of the Permian red beds. The beach/dune faunas of the Coconino and De Chelly Sandstones (both of Arizona) and of the Lyons Sandstone (Colorado) "are quite unlike those from Cutler [Formation of Colorado] and other contemporary red beds; their affinities lie rather with Permian dune-sand footprints from Great Britain . . . and the Cornberger Sandstein of Germany Footprints made in sloping sand are much more difficult to interpret than those made on mudflats, but so far as I can see the ichnofaunas of red beds and dune sands have nothing in common." Baird (written commun., 1984) has elaborated:

" . . . the Hermit-Supai ichnofaunas appear to be standard Texas/New Mexico redbeds assemblages whereas that of the Coconino/De Chelly/Lyons is quite different not only in facies (dune sand) but in faunal content. That's why Lull and Gilmore went wrong in comparing Coconino tracks with taxa from the Permo-Carboniferous coal swamp and redbeds facies: the cast of characters is almost completely different. My strong suspicion is that the ichnofauna of the Coconino (et al.) represents E. C. Olson's caseid facies-fauna, which infiltrated Texas from somewhere and gradually replaced the old redbeds assemblage."

McKee (1982, pp. 91-93) observed that the vertebrate tracks of the Wescogame Formation of the Grand Canyon (i.e., the Supai trackways) occur in foreset beds and slabby sandstones--even on a ripple-marked surface. As such, the Wescogame ichnites' environment of deposition differed from those of the red-bed Hermit Shale and the desert-dune Coconino Sandstone. Therefore, there are three principal types of terrestrial/streamway ichnofaunal paleoenvironments in the Grand Canyon: 1) desert dune, hosting the Coconino ichnofauna of reptiles and scorpions, 2) red-bed muds, hosting the Hermit ichnofauna of reptiles and amphibians, and 3) underwater and wet sands, hosting the Wescogame ichnofauna of reptiles and amphibians. As noted, the Hermit and Wescogame ichnofaunas are taxonomically related, so the different host lithologies bring attention to the role of depositional environment in the taphonomic history of ichnites: whereas the Hermit and Wescogame Formations are both red bed units, the preferential distribution of Wescogame ichnites in sand beds in that formation points to facies control in the taphonomic processes there.

Virtually all of the Pennsylvanian-Permian ichnofaunas of the Grand Canyon are restricted to one of the three formations mentioned here. This lack of stratigraphic distribution most likely represents contemporary environmental controls in the creation and preservation of the tracks, not a real restriction of the original animal species to these periods. Only one species--*Batrachichnus delicatulus*--is found in more than one formation; it occurs in the Hermit Shale and the Supai Group (Wescogame Fm.). Baird (in Breed, 1967), as mentioned in the text, has already explained this occurrence as *de facto* evidence of Permian Hermit-type animals having been present during Pennsylvanian Supai time. This is a problem met when dealing with a very incompletely understood ichnofauna, one known only from scant fossil evidence.

The chart on the facing page supplements Table 4, illustrating the stratigraphic distribution of the identified ichnites of the Wescogame Formation, Hermit Shale, and Coconino Sandstone.

Stratigraphic Distributions of Identified Ichnites

| Stratum | | Locality | Hermit Trail | | | | | | | | | | Bright Angel Trail Wescogame Fm. | South Kaibab Trail | | Grandview Trail Coconino Ss. | Stanton's Cave Wescogame Fm. | | |
|----------|--------|----------|--------------|------------------|-----|-----|-----|----|------------|---------------|------------|---------------|-------------------------------------|--------------------|---|---------------------------------|---------------------------------|----|----|
| Coconino | Hermit | | Wescogame | Coconino Ss. | | | | | Hermit Sh. | Wescogame Fm. | Hermit Sh. | Wescogame Fm. | | | | | | | |
| | | | | 150 | 130 | 125 | 100 | 30 | | | | | | 20 | ? | | | 40 | 30 |
| | | | | | | | | | | | | | | | | | | | |
| Fossil | | | Stratum | (ft. above base) | | | | | | | | | | | | | | | |
| | | | Horizon | | | | | | | | | | | | | | | | |
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Notes:

F = occurrence as float

The Stanton's Cave specimen of *Batrachichnus delicatulus* is noted by Baird (in Breed, 1967) to occur in Supai-type sediments. Although it is a reasonable assumption that the original horizon was the track-bearing stratum of the Wescogame Formation, the Supai environment of deposition on the karst surface of the Redwall Limestone was a process of depression-infilling and/or karst collapse. The horizon of *B. delicatulus* at Stanton's Cave cannot therefore be established with certainty, but it is plotted herein as the Wescogame Formation.

5) "*Collettosaurus pentadactylus* has nothing to do with *Collettosaurus* Cox, 1874, nomen dubium. Cox's description is hopelessly wrong and the type specimen is lost . . ." (1983).

6) "Gilmore was on the right track in comparing his new *Hylopus hermitanus* with *Hylopus hardingi* Dawson, but mistaken in thinking *hardingi* to be the type species. The type species, *H. logani*, is Lower Mississippian and quite different. I would transfer both *hardingi* and *hermitanus* to *Palaeosauropus*, but haven't yet done so in print" (1983). [*Palaeosauropus* Hay, 1902.]

The most recent zoologic reference to any of the Grand Canyon ichnogenera was by Briggs & Rolfe (1983), who compared a giant arthropod trackway (the new species *Palmichnium kosinskiorum* from the Lower Mississippian of Pennsylvania) to *Paleohelcura* Gilmore (from the Grand Canyon). Briggs & Rolfe's (1983, p. 388) emended definition of *Palmichnium* Richter states that this ichnogenus "differs from the smaller and differently proportioned *Paleohelcura* . . ." They continued, "While it is theoretically likely that a series of intermediates between the two forms exists, it is considered useful to maintain the separation between them as they arguably represent two extremes; *Paleohelcura* is probably the result of the normal gait of a scorpion and *Palmichnium* the unusual gait of an amphibious eurypterid out of water."

Briggs & Rolfe (1983) also remarked on the Permian "spider" trackway described by Alf (1968) from the Coconino Sandstone at Seligman, Arizona. They said (p. 387), "Alf's trackway can be referred to *Octopodichnus*, with some enlargement in the concept of this ichnogenus." However, no mention was made of Brady's (1947, p. 468) remark, "In view of the . . . variations in the track of *Octopodichnus* observed in the study of over a dozen specimens it would seem advisable to make some change in the generic definition," which then followed. Brady included *Octopodichnus* with question in the Scorpionida.

Obviously, whoever takes on the task of re-studying the Grand Canyon ichnofauna must immediately address the prospect of many nomenclatural revisions. Miller *et al.* (1982, pp. 6-15) discussed the sorry state of the Grand Canyon fossil herpetofauna, but they did not make note of any of Baird's reassignments. They concluded (p. 14): "Unless substantiative evidence [from other late Paleozoic ichnite localities] is introduced, the Paleozoic ichnite faunas of the Grand Canyon will remain poorly understood, though certainly no less intriguing."

ORIGIN OF THE TRACKS. The techniques of creation and preservation of the Grand Canyon ichnites has been a matter of considerable interest and experimentation, particularly about the ichnites of the Coconino Sandstone desert dunes. But not many studies have been made on the formation and preservation of the Hermit-Supai tracks. Peabody (1956) published a short description of

the peculiar trackway of *Hyloidichnus bifurcatus* Gilmore in which he compared the footprints to those of the modern arboreal salamander *Aneides lugubris*. He remarked that a split-toed footprint like that of *H. bifurcatus* could have been made by truly bifurcated toes, but preferred an empirical comparison with the tracks made by an amphibian moving at an accelerated pace.

As mentioned earlier, virtually all of the ichnites in the Coconino Sandstone point upslope on the dune faces. This trait has been well studied. Gilmore (1926b, p. 4) suggested that this might indicate "an old trail leading to water, or possibly recording a great migration of animal life . . ." McKee (1933, p. 108) more seriously addressed the phenomenon, stating "that probably this peculiar feature is not the result of any unusual condition, but that it is due to a natural coincidence between the movements of the animals and the dampness of the sand." First dampened by "rains, dews, or any other agency," the sands thus would have better suited preservation and recovery of the footprints by permitting sharper definition of parting planes in the lithified sediments. This premise has withstood subsequent empirical studies, although it appears that many modes of preservation may be responsible.

Reiche (1938) reported that he had observed on the lee slopes of rain-dampened modern dunes the uphill-pointing tracks of coyotes, rabbits, and lizards; downslope tracks had been obscured by sliding sand. This short remark was, as will be discussed in the following paragraphs, partly accurate in its application to the fossil tracks of the Coconino.

Brady (1939) reported the results of the first empirical experiments on the formation and preservation of the Coconino ichnites. Sand surfaces were prepared with varying degrees of wetness and inclination, after which living arthropods were induced to walk upon the sand. Mature individuals of the scorpion *Centruroides sculpturatus* created tracks like those of *Paleohelcura* Gilmore. An undescribed fossil track resembled that made by the isopod crustacean *Uniscus*, resembling Early Cretaceous *Archaeoniscus*. (*Archaeoniscus* is not mentioned by Häntzschel, 1975.) Perhaps the most significant observation made by Brady, though, was his discounting the hypothesis that the tracks were made and preserved during early morning dampening by dew. His experiments showed that the Coconino tracks could have been made nocturnally, later dampened by morning dew, and preserved by being buried before drying.

McKee (1944, 1947a) followed up on these studies, empirically producing lizard and millipede tracks on various substrates. He sustained Brady's findings for a dry-sand origin for the tracks, subsequently dew- or mist-dampened prior to burial and preservation. Tracks made by lizards walking on wet sand differed according to the weight of the animal; very small ones left

only toe scratches. Many of the tracks produced experimentally did not resemble the fossil tracks of the Coconino. Most significantly, the phenomenon of uphill-pointing tracks was studied, with a rather simple explanation forthcoming (as already implicated by Reiche, 1938). The experiments with living animals demonstrated that tracks made while moving downslope were largely eradicated by slumping of the sand during the animals' movements. Also notable was the formation of millipede tracks only on lower-angle slopes; millipedes could not ascend steep slopes of dry sand. McKee summarized that the mystery of fossil track preservation remained mostly unsolved, but that the Coconino tracks were apparently formed mostly on dry, loose sand on high-angle slopes such as those on the lee sides of dunes.

Brady's (1947) paper on some of the northern Arizona ichnites is devoted mostly to comparisons between fossil specimens and tracks made by living animals. He repeated his earlier assertion (Brady, 1939) that tracks made under controlled conditions by the modern scorpion *Centruroides* are like those of the fossil *Paleohelcura*. Based on morphologic variations seen among some of Gilmore's Grand Canyon fossils and among the tracks of living scorpions, Brady concluded that both *Paleohelcura* and *Octopodichnus* should probably be referred to scorpionids. He summarized (pp. 467-468):

"It seems . . . very doubtful that any new species should be erected for such variations, which may well be due to differences of temperature, surface condition and slope, and possibly the disposition of the animal In this connection it may be noted that in experimental work of this kind, live scorpions are extremely uncooperative."

Until recently, the studies by Reiche, Brady, and McKee were the only attempts to analyze the conditions of formation and preservation of dune-face trackways. Sarjeant (1975), in a short review of the hypothetical conditions for preservation of the Coconino ichnites, cited only Reiche (1938) and McKee (1944) and presented no new remarks on the method of preservation. Brand (1978, 1979), however, published new experimental evidence that not only pointed to a subaqueous environment for the formation of the Coconino quadruped ichnites, but that the ichnites should not be used at all as indicators of an eolian environment of deposition for the Coconino. Studying the tracks made by amphibians and reptiles on dry, damp, wet, and underwater sands, Brand observed that dry-sand tracks showed only depressions and that underwater tracks most resembled the Coconino ichnites. He rejected the obscured-track explanation for the virtual absence of downhill-pointing fossil tracks, stating that under all of his laboratory conditions downhill tracks were produced successfully. Although not as well defined as the laboratory uphill-pointing tracks, the laboratory downhill tracks were "more

distinct than many of the fossil tracks" (Brand, 1978, p. 81). However, Brand did not offer any explanation for the absence of downhill fossil tracks except simply that the animals probably swam above the bottom while moving with the water current (while movement upstream required traction, hence sure planting of feet). One remark Brand (1978, p. 81) made is nonetheless accurate and wholly applicable to the study of all ichnites: "Behavioral traits of extinct animals cannot be tested, but . . . behavior can affect the tracks under water in ways that are not possible above water."

Even though some workers may take issue with Brand's conclusion, and may find fault with his lithologic interpretations of the environments of deposition of the Coconino Sandstone, his experiments do present a valid alternate hypothesis to this long-running subject of discussion. But, in presenting a potential objection to his observations and conclusions, Brand (1979, p. 37) made an inappropriate remark on the previously collected Coconino specimens:

"One objection that could be made to the data used in this paper is that many fossil trackways have been removed from the Hermit Basin and deposited in museums, and consequently I studied a biased sample. * * * . . . in choosing specimens for museums, it is likely that some preference would be given to the better preserved tracks If these specimens had been included in my sample, it would only have increased, rather than decreased, the difference between the fossil tracks and the dry sand and damp sand tracks."

Brand studied the Coconino ichnites *in situ* along Hermit Trail, and he was at fault for not also studying first-hand the previous collections of fine Coconino tracks. He was probably correct in suspecting in the early collections a bias for the taxonomically more identifiable specimens. But Gilmore (1927a) was quite specific in identifying another, more determinant, bias which Brand overlooked. Because of this, Brand may have unknowingly studied some of the best specimens:

"While slabs of considerable size were collected, larger and more impressive trackways might have been secured but for the difficulty of transporting them to the top of the Canyon, as all of these specimens were brought out of the Canyon on mule back along a narrow and often precipitous trail. It will thus be seen that the size of the specimens collected was always determined by the carrying capacity of a mule, which is about 150 pounds on these trails" (Gilmore, 1927a, p. 48).

From the first two ichnite collecting expeditions alone, in 1924 and 1926, Gilmore secured 4,400 pounds of material for the U.S. National Museum

(Gilmore, 1927c)--about 30 fully loaded mules.

The Coconino Sandstone has, both on paleontological and lithological grounds, long been considered to be an eolian sandstone. McKee with Bigarella (1979) convincingly summarized the criteria for interpreting an eolian origin of the Coconino, although preparation of that paper preceded the publication of Brand's reports.

McKee (1982) discussed the distribution and age of the vertebrate ichnites of the Wescogame Formation. The known ichnofauna consists of four of Gilmore's taxa: "*Ammobatrachus turbatans*," *Anomalopus sturdevanti*, *Stenichnus yakiensis*, and *Tridentichnus supaiensis*; but, as McKee pointed out, the nature of the animals that made these tracks is not known. McKee did refer, without discussion but with an accompanying figure, to underwater tracks made by a large amphibian in unpublished laboratory experiments by Brand; these tracks resemble some fossil tracks seen along South Kaibab Trail.

HOPEFUL PROSPECTS. It is clear from this lengthy discussion that not only are the Grand Canyon ichnofaunas peculiar, but there is little hope for any immediate clarification of their zoologic nature. The principal fault here is the paucity of specimens in the fossil record. Without substantial evidence, either from fossils or from living comparative animals, the existing collection is doomed to remain intriguingly ambiguous; and the taxonomic nomenclature suffers for it. Perhaps more decisive inroads will be made toward understanding the paleozoologic position of the Grand Canyon ichnofaunas. For the time being, though, we must continue to track the literature for discoveries and new interpretations that might have applications to studies of the Grand Canyon fossils.

Paleozoic Floras

Fossil plants have been reported from Arizona since 1850, but the impressive Mesozoic floras, including that at the spectacular Petrified Forest National Park, have generally overshadowed the Late Paleozoic assemblages. (For a concise history of Arizona paleobotany, see Romans, 1973.) All kinds of fossil plant material are found throughout the Grand Canyon strata, but fossil land plants were not known from the Canyon until 1916, when L. F. Noble made the first collection in the Hermit Shale.

Real or presumed algal forms are noted throughout most of the Paleozoic strata. Among these is *Rivularites* Fliche, 1906, a genus considered by many investigators to be a primary sedimentary feature and therefore inorganic (e.g., Fenton, 1946; Häntzschel, 1962, 1975; Kummel & Teichert, 1970; Teichert, 1970). White (1929a) named a new species of *Rivularites* from the Permian of the Grand Canyon, *R. permiensis*. Häntzschel (1962, p. W236), in remarking on *Rivularites* in general, singled out *R. permiensis* as a specific example in declaring the genus a sedi-

mentary feature "very similar to mud flow markings on bedding planes." Later, Häntzschel (1975, p. W179) was more emphatic, revising the description to read, "bedding plane features doubtlessly inorganic in origin, very similar to mud flow markings." He probably was influenced by the diagnoses of Kummel & Teichert (1970) and Teichert (1970). Kummel & Teichert (1970, p. 40) likened *Rivularites* to "capped interference ripples"; but Teichert (1970) revised the interpretation, calling these same features "*Runzelmarken* (wrinkle marks)," surfaces of wet, fine-grained sediments that were nearly or completely exposed to wind. But *Rivularites* continues to be reported from the Grand Canyon strata as an algal genus. McKee's (1982) monograph on the Supai Group, the product of more than 50 years of study, partly predates the biological discussions on the affinity of *Rivularites*. Yet, McKee's observations of *Rivularites* sp. as an alga are compatible with the observed paleoenvironments. Outrightly discarding the algal interpretation of the genus might be hasty.

A variety of late Paleozoic land plants have been reported from Chesterian-age pre-Supai channel deposits of western Grand Canyon, from the Supai Group, and from the Hermit Shale. The Early Permian flora of the Hermit comprises a unique assemblage that will be discussed in the next section.

The Chesterian channel deposits in the top of the Redwall Limestone contain poorly preserved plants and algae. Billingsley & McKee (1982, pp. 139, 141, 143, quoting a 1978 written communication from S. H. Mamay) recorded from the sandstone facies of the "lower unit" two specimens of a fern ("a very delicate, small-pinnuled sphenopterid or pectopterid"), five sphenopsid fragments ("parts of the fruiting organs of a phyllotheoid plant"), and "several unidentified axial scraps." An examination for palynomorphs in the "lower unit" by R. M. Kosanke was also reported by Billingsley & McKee (p. 143): 14 palynomorphs were identified to species (in 10 genera), and seven to genus; also noted were monosaccates and unassigned ("algal") remains. In the "upper unit," the only plant fossil is the green alga *Ortonella* sp.; no plants are reported from the "middle unit" (Billingsley & McKee, 1982).

Although the larger plant fossils of the Chesterian sediments are fragmentary and unsuited to studies of correlation and age, the palynomorphs (together with the foraminifera already mentioned in the section on Paleozoic invertebrates) have already proven to be instrumental in establishing the Late Mississippian age of the channel deposits. The crucial palynomorph indicator species are *Anaplanisporites globulus*, *Aurorospora solisortus*, and *Hadrohercos stereon*, used by some researchers as Late Mississippian index fossils (Billingsley & McKee, 1982).

In 1936, White summarized (p. 685) that "Little is known of the floras of the lower por-

tion of the red-bed series in northern Arizona," despite even his detailed studies in the area. McKee's (1982) Supai monograph indicates, however, that fragments of land plants are stratigraphically and geographically scattered throughout the Supai Group. These fragments are stems, leaves (ferns), and miscellaneous pieces.

White (1928a) briefly remarked that he had identified *Walchia*, *Cordaites*, and *Calamites* in a stratum 60 ft above the base of the Supai; and in his Hermit flora monograph (White, 1929a, p. 39) he added *Neuropteris* and *Taeniopteris* to that list of basal Supai plants. Blazey (1971), in his dissertation on the Mogollon Rim fossil flora of central Arizona, cited only White's three 1928 basal Supai plant genera, commenting (p. 43), "The fossil representatives are disappointingly meager but suggest that a flora similar to the Rim flora may be present in the Grand Canyon in this stratum."

A few of the Supai plants are useful as indicators of age and of depositional environment, although none have been crucial in such roles. The upper limit of the Esplanade Sandstone and of the Pakoon Limestone with which the Esplanade intertongues, is in turn fixed by the age of the flora of the overlying Hermit Shale. White (1929a) pinpointed a late Early Permian age for the Hermit. McKee's (1937a) discovery of diagnostic Early Permian Hermit plants above the Esplanade Sandstone in western Grand Canyon established that the stratum of the Hermit Shale flora could be used, at least in the Grand Canyon, as a time-stratigraphic boundary. By default, the Esplanade-Pakoon rocks must all be of Early Permian age. McKee (1982) further substantiated this view by citing invertebrate paleontologic evidence from Early Permian faunal assemblages in western Grand Canyon and Nevada.

Algae, including *Rivularites* and stromatolites, are found throughout the Supai Group (McKee, 1982). Elsewhere in the Grand Canyon strata, various algal forms have been recorded. They, like the Supai plants, are useful in analyzing depositional environments, although none of them are important diagnostic elements.

Among workers who favor Creationist viewpoints on the diversity of ancient life, Burdick (1966) reported having found pollen grains of modern affinities in the late Precambrian Hakatai Shale, Cambrian Bright Angel Shale, Mississippian Redwall Limestone, and Permian-Pennsylvanian Supai Group. These claims for flowering plants as early as the late Precambrian sparked among Creationists a flurry of excitement, fanned by Burdick's (1972) progress report which said repetition of the 1966 procedures practically duplicated the earlier results. Burdick (1972, p. 26) concluded that "gymnosperms (conifers) were a dominant type of plant or tree in the Permian, Mississippian, Cambrian, and younger Precambrian." This he had taken (Burdick, 1966) as evidence of all of the Grand Canyon strata having been formed in a relatively short period

of time. Chadwick *et al.* (1972) replied to Burdick's citation of work done by them, stating, "... our findings neither confirm nor refute Burdick's major conclusions. The current work is adding detailed information which indicates that the pollen story is more complex than previously pictured." Chadwick (1981) reviewed the status of studies on the Grand Canyon pollens and investigated the possibility that Burdick's specimens had been contaminated by modern pollens. Burdick's localities were revisited, new specimens collected, and, with care taken to remove all possible contaminants, the samples were prepared and examined in the laboratory. Of 50 samples, Chadwick (1981, p. 8) reported, "No single example of an authentic pollen grain was obtained"

The Hermit Shale Flora (Early Permian)

Prior to David White's studies of the Hermit Shale, conducted during the mid- to late-1920s under the auspices of the Carnegie Institution of Washington, the ages of the late Paleozoic Grand Canyon formations were loosely considered to be Pennsylvanian to Permian. Bounded by the Supai formation (of contemporary usage) and the Kaibab formation (which had not yet been divided into Kaibab and Toroweap Formations), the Hermit Shale and Coconino Sandstone were not convincingly correlated with precisely dated rock units elsewhere. By lithostratigraphic correlation, the Supai was assigned a Pennsylvanian age; but the Kaibab, while lithostratigraphically apparently Permian, included a problematical "Pennsylvanian" molluscan fauna. White's (1927a, 1928a, 1929b) preliminary reports to the Carnegie Institution quickly pinpointed a late Early Permian age for the Hermit Shale flora, and his monograph (White, 1929a) meticulously put the stratigraphic picture in perspective. With the Hermit Shale being Early Permian, the overlying Coconino and Kaibab formations, by default, had to have Permian ages. Hence, riparian plants of the Hermit dated an eolian, full-desert, paleoenvironment of the Coconino.

The first of the Hermit Shale plants were collected in 1915 by Charles Schuchert who passed the specimens along to David White, Chief Geologist at the U.S. Geological Survey and Curator of Paleobotany for the U.S. National Museum. After additional plants had been collected by L. F. Noble in 1916, White that year wrote to Schuchert that he had identified *Gigantopteris*, *Walchia*, and *?Callipteris* among the poorly preserved specimens (Schuchert, 1918a, p. 354). White went on in his letter to specify an Early Permian age of the flora--or at least certainly not earlier than latest Pennsylvanian. (The Hermit Shale had not yet been named; it was at that time the upper part of the Supai formation.)

White's interest in the Hermit flora was given another boost when in 1920 Noble forwarded to him still more material from the Hermit Shale.

The potential importance of the flora to stratigraphic and evolutionary studies convinced the Carnegie Institution of Washington to support three summers of collecting at the Grand Canyon. White led these expeditions in 1926, 1927, and 1928. In retrospect, we can note that all of the Hermit plant specimens were found in the Hermit Basin and along Bright Angel and Yaki (South Kaibab) Trails; but by far the most productive localities were in the Hermit Basin, particularly along Hermit Trail. The first fruits of these labors were reported by Sturdevant (1926a), who observed that a collection from along Hermit Trail contained three species of ferns, including a remarkable nearly complete specimen in a slab about two feet square and another specimen apparently preserved in an upright position. Sturdevant declared the collection "the best yet made."

The first formal findings on the Hermit flora were presented to the National Academy of Sciences (White, 1927b). In this preliminary report, White said (p. 575), "The Hermit plants embrace a number of European conifers and fern-like seed-bearing plants (pteridosperms) found in Europe or closely related to European species, but about half of the flora has not been known before." He also remarked that some forms were "Uralo-Asiatic in character." Although White did not specify which known genera he had found, he noted particularly that all Calamarian types and the cosmopolitan genera *Neuropteris*, *Alethopteris*, and *Pecopteris* were apparently absent from the Hermit flora. This he attributed to the unfavorable (dry) paleoenvironment. He went on to mention that the closest North American match to the Hermit floral assemblage was that of the Wellington Formation of Kansas (Early, but not earliest, Permian).

In a progress report, White (1927a) for the first time since his 1916 correspondence with Schuchert mentioned one of the three genera (*Walchia*) he initially saw in the Hermit collection, although he also referred to a "single species" of *Sphenophyllum* and in group senses to "Callipterids" and "Taeniopterids." (White later stated [1929a, p. 3] that the inaugural collection contained *Callipteris*, *Sphenophyllum*, and *Walchia*, and that what he had identified as *Gigantopteris* was probably referable to his new genus, *Supaia*.)

White's (1929a) definitive monograph finally listed all the discernible plant taxa of the Hermit Shale: 32 species (25 new) in 15 genera (three new), 10 specimens identified only to genus, and "a poorly preserved ament, probably belonging to a gymnosperm" (p. 115). The new genera were *Supaia* (9 species) and *Yakia* and *Eltovaria* (both monospecific). The plant groups represented in the flora are the thallophytes (*Rivularites*, which is presently treated by most workers as a sedimentary feature), arthropytes (*Sphenophyllum*), pteridosperms (*Callipteris*, *Supaia*, *?Brongniartites*, *Yakia*, *?Neuropteridium*, *Taeniopteris*), ginkophytes (*Psygmyphyllum*),

conifers (*Walchia*, *Ullmannia*, *Voltzia*, *Paleotaxites*, *?Taxites*, *Brachyphyllum*, *Pagiophyllum*), and fruits of uncertain affinities (*Cyclocarpon*, *Carpolithus*, *Eltovaria*). Through White's interpretations of the character of the flora and the sediments in which the plants are found, the Early Permian environment was pictured as a semi-arid climate with long, hot, dry seasons. Paleomagnetic studies of some of the Grand Canyon formations have since borne out White's analyses: during the Permian, Arizona was just to the north of the equator (Cox & Doell, 1960; Creer *et al.*, 1957; Doell, 1955; Runcorn, 1955, 1956).

The discovery of the Hermit flora was a fortuitous event in the advancement of paleobotany. White (1929a, p. 40) quickly pointed out that not only did this collection represent the youngest American Paleozoic flora known at that time,* but "the presence also of both Gondwana plants and plants of distinctly Mesozoic aspect" placed the flora in a key position in world and stratigraphic paleobotany. The deceptively Mesozoic aspect of the plants White attributed to climatic factors of the Hermit paleoenvironment. That most of the observed species were new was at that time academic; surely, White held, these, related, and new species would turn up in future studies at the Grand Canyon and elsewhere. But such optimism was in vain. Although late Paleozoic floras of the world are on the whole strikingly similar, almost all of the species unique to the Hermit Shale in 1929 are still paleobotanically alone; and some of these species are still represented by unique specimens.

In 1933, White presented to the 16th International Geological Congress a review of the Early Permian flora of America. In that paper (White, 1936), the Hermit flora assumed its proper place among the other Permian floras--as a little-understood assemblage that had received a great deal of academic attention. On the basis

*The youngest known North American Permian megafloora, of late Leonardian age, has recently been reported from the Del Norte Mountains of Trans-Pecos Texas (see Mamay *et al.*, 1984). It is an important discovery because the locality contains abundant plant fossils, and identifiable plant megafossils were heretofore scarce not only in the standard North American Permian section of West Texas but in other late Leonardian North American strata as well. The Permian paleobotanical material of the Grand Canyon and other, scattered North American localities have documented several floral provinces and stratigraphic floral zones (cf. Read & Mamay, 1964), but all are older than the newly found flora. The Del Norte flora has been so precisely correlated with other dated units of the standard Permian section through the conodont fauna found in association with these plants. Except for *Taeniopteris*, none of the reported Del Norte plant genera are represented among the known Grand Canyon Hermit Shale plants, although wholly excluding them at this early date would be premature. Still, Mamay *et al.* (1984, p. 279) pointed out that "the Del Norte leaves are the most spectacular and phylogenetically enigmatic foliar organs in all of the American Paleozoic." David White's Hermit Shale plants had their brief stay in the paleobotanical limelight before being academically placed aside as frustratingly unique; now they are joined in fame by another enigmatic Permian flora, although one that is younger and composed mostly of recognizable genera. Continued research and fortuitous discoveries of new fossil plant localities may yet lead to a better understanding of the Hermit paleoflora.

of fossil floras, White drew up a tentative correlation chart for the Permian and Pennsylvanian strata of the Midcontinent and Rocky Mountain regions. In the chart, the Hermit Shale is correlated with the middle of the Chase Group of Kansas and northwestern Arkansas. The Chase Group is below the Wellington Formation (Summer Group), the flora of which White (1927b, 1929a) had earlier compared with part of the Hermit flora. White's chart specified that the Wellington is approximately equivalent in age to the lower Kaibab limestone (i.e., late Early Permian Toroweap Formation). More recent usage (Permian Subcommittee, 1960) correlates the early Leonardian Wellington with the Hermit, and the late Wolfcampian Chase Group with the upper part of the Supai Group. Swanson *et al.* (1981), indicating official usage conventions of the U.S. Geological Survey, retain the Hermit Shale, the Wellington Formation, and the Chase Group only as "Lower Permian," without any further refining to stratigraphic Stage names.

After White's monograph was completed, original research on the Hermit Shale flora virtually ended. White (1934) published an abstract in which he recorded the first seed-bearing specimen of *Supaia*, from the Supai formation of southern Arizona's Apache Indian Reservation. McKee (1937b, p. 341) reported a still-unpublished collection of plants from the Hermit Shale at Parashant Canyon; that collection contained "*Gigantopteris americana*, as well as several well-known Hermit species."

White's unfigured seed-bearing *Supaia* ostensibly proved *Supaia* to be a pteridosperm, but the specimen is apparently missing (Mamay & Watt, 1971). Mamay & Watt (1971), however, described a single "seed-bearing fragment of a *Supaia*- or *Callipteris*-like frond" that had been found in 1952 near White's Hermit Trail locality. They remarked that, "in the absence of White's specimen, this fragment is the only ovuliferous pteridophyll specimen known from the *Supaia* flora . . ." (p. C48). Except for that short paper, no other new paleobotanical work has been published on the Hermit flora of the Grand Canyon; nor for that matter has White's collection been restudied. (See Table 5 for a list of the current status of the known Hermit Shale paleoflora.)

The most recent comparison to the Hermit Shale flora of the Grand Canyon is the Mogollon Rim study by Blazey (1971, 1974), who described the fossil flora of the Mogollon Rim area of central Arizona. Blazey (1971, p. 42) remarked on the Hermit collection: "Although this flora could stand a modern revision, additional information would not alter its character. Only one common species and 3 common genera [of the Grand Canyon Hermit flora] are shared with the Mogollon Rim flora; these are: *Sphenophyllum*, *Taeniopteris*, *Walchia piniformis*, and *Callipteris*." However, these remarks were editorially(?) omitted from the published version (Blazey, 1974) of Blazey's dissertation.

Even though the Hermit Shale paleoflora has been largely unstudied since 1929, this is not to say that it has gone unnoticed; *Supaia*, particularly, has been widely recognized and studied. The *Supaia* floral province has been established as one of three floral provinces of the Leonardian of the Southwest; the other two are those of *Gigantopteris* and *Glenopteris* (Mamay, 1976). These three provinces comprise Read & Mamay's (1960, 1964) stratigraphic floral zone 14, which extends from Kansas, Oklahoma, and northern Texas into New Mexico and Arizona. Floral zone 14 includes: an older-*Gigantopteris* floral zone in parts of Texas, Oklahoma, and New Mexico; an equivalent zone of *Glenopteris* spp. in Kansas; and the zone of *Supaia* spp. in Arizona (Read & Mamay, 1964). Mamay & Breed (1970) reported an extension of the *Supaia* floral zone, represented by a Hermit-like flora in the Permian Cutler Formation of Utah. *Supaia rigida* White, *Taeniopteris* sp., and *Callipteris*? sp. are the Hermit-like representatives of this flora; but the presence of *Protoblechnum* Lesquereux, represented by Mamay & Breed's new species *P. bradyi*, indicates an Asiatic relationship (Mamay & Breed, 1970).

The *Supaia* flora, composed of about 20 plant genera (Read & Mamay, 1964), existed to the west of the ancestral Rocky Mountains in an ecologically harsh region (Read & Mamay, 1964; Mamay, 1976). The precise number of constituent genera within the *Supaia* flora is in question because of the poor preservation of most of the material: "a more realistic appraisal of the flora would likely yield no more than half as many generic designations" (Read & Mamay, 1964, p. K13). The arthropytes of the *Supaia* flora are represented only by *Sphenophyllum gilmorei* White (which, without discussion, Darrah [1969] said is a reliable Permian stratigraphic indicator species in the United States); the conifers, mostly *Walchia*, are unremarkable; and some callipteroid species are probably referable to *Supaia* (Read & Mamay, 1964). *Taeniopteris*, however, was a "chronologically persistent, geographically adventuresome, and ecologically resilient" member of the *Supaia* flora; it is conspicuous in all three of the Leonardian floral provinces of the Southwest (Mamay, 1976, p. 29).

Callipteris arizonae White, one of the new species to come out of the Hermit Shale, has also been reported from the Leonardian Bone Spring Limestone of southeastern New Mexico (McKee, 1967, p. 215). Before the Bone Spring specimen was found, the species was known only by a unique specimen. Discovering a second occurrence of the species in Leonardian rocks some distance from the Grand Canyon was a reconfirmation (albeit superfluous) of White's definitive placement of the Hermit Shale in the Early Permian.

Overall, the Southwest is an important area to the study of Early Permian paleobotany, even if the fossil record is not as good as we might wish it to be. Mamay (1976, p. 44) summarized that the "Lower Permian deposits of the southwestern United States contain proof that this

Table 5. The Early Permian Hermit Shale Flora of the Grand Canyon¹

| Name | Grand Canyon Type Fossil No. ² | Description in White (1929a) (page nos.) | Grand Canyon Hermit Shale Localities ³ | Remarks |
|--------------------------------------|--|--|---|---|
| <u>Arthrophytes</u> | | | | |
| <i>Sphenophyllum</i> Koenig, 1825 | | | | |
| <i>S. gilmorei</i> White, 1929 | 152 | 44-47 | HB, BA, SK | |
| <u>Pteridosperms</u> | | | | |
| <i>Callipteris</i> Brongniart, 1849 | | | | |
| <i>C. conferta</i> (Sternberg), 1825 | -- | 47-50 | BA, SK | |
| <i>C. arizonae</i> White, 1929 | 153 | 50-52 | HB | |
| <i>C. raymondi</i> Zeiller, 1896 | -- | 52-53 | HT, BA | |
| <i>C.?</i> sp. | -- | 53 | HB | |
| <i>Supaia</i> White, 1929 | | | | Designated the genotype species. |
| <i>S. thimfeldioides</i> White, 1929 | 154 | 54-62 | HB | |
| <i>S. anomala</i> White, 1929 | 155 | 62-64 | HB, BA | |
| <i>S. breviloba</i> White, 1929 | 156 | 71-72 | HT, BA | |
| <i>S. compacta</i> White, 1929 | 157 | 74-75 | HB | |
| <i>S. linearifolia</i> White, 1929 | 158 | 69-71 | BA | |
| <i>S. merriami</i> White, 1929 | 159 | 72-74 | HB | |
| <i>S. rigida</i> White, 1929 | 160 | 67-69 | HT | |
| <i>S. sturdevantii</i> White, 1929 | 161 | 64-65 | BA | |
| <i>S. subgoeppertii</i> White, 1929 | 162 | 65-67 | SK | |
| <i>S.</i> sp. | -- | 75-77 | HB | |
| <i>S.</i> sp. indet. | -- | 77-78 | HB | |
| <i>S.?</i> sp. | -- | 78 | HB | |
| | -- | 78-79 | SK | |
| Seed | | | | |
| | -- | -- | HB | A single "seed-bearing fragment of a <i>Supaia</i> - or <i>Callipteris</i> -like frond" (Mamay & Watt, 1971, p. C48). |
| <i>Yakia</i> White, 1929 | | | | |
| <i>Y. heterophylla</i> White, 1929 | 163 | 86-91 | HB, BA | Genotype by original monotypy. |

| | | | | |
|--|-----|---------|---------------|----------------------------|
| <i>Brongniartites</i> Zalesky, 1927 | | | | |
| <i>B. ? aliena</i> White, 1929 | 164 | 84-86 | SK | |
| <i>B. ? yakienais</i> White, 1929 | 165 | 79-84 | HT, SK | |
| <i>Neuropteridium</i> Schimper, 1869 | | | | |
| <i>N. ? sp.</i> | -- | 91-92 | BA | |
| <i>Taeniopteris</i> Brongniart, 1928 | | | | |
| <i>T. cf. eckhardti</i> Kurtze, 1859 | -- | 92-93 | HT, BA | |
| <i>T. angelica</i> White, 1929 | 166 | 93-94 | BA | |
| <i>T. coriacea</i> Goepfert, 1864 | -- | 94-95 | DS, BA | |
| <u>Gymnosperms</u> | | | | |
| <i>Psugmophyllum</i> Schimper, 1872 | | | | |
| <i>P. ? sp.</i> | -- | 95-96 | HB | |
| <i>Gigantopteris</i> Schenck, 1883 | | | | |
| <i>G. americana</i> White | -- | -- | PC | Cf. McKee (1937b, p. 341). |
| <i>Gymnospermous ament</i> | | | | |
| | -- | 115 | Not specified | |
| <u>Conifers</u> | | | | |
| <i>Volzia</i> Brongniart, 1828 | | | | |
| <i>V. dentiloba</i> White, 1929 | 167 | 105-106 | HT | |
| <i>V. sp.</i> | -- | 106 | Not specified | |
| <i>Walchia</i> Sternberg, 1826 | | | | |
| <i>W. piniformis</i> (Schlotheim), 1820 | -- | 96-99 | HB, BA, SK | |
| <i>W. dawsoni</i> White, 1929 | 168 | 99-100 | HB | |
| <i>W. gracillima</i> White, 1929 | 169 | 100-101 | SK | |
| <i>W. hypnoides?</i> (Brongniart), 1828 | -- | 102 | Not specified | |
| <i>Ullmannia</i> Goepfert, 1850 | | | | |
| <i>U. frumentaria</i> (Schlotheim), 1820 | -- | 102-105 | HT, BA | |

Table 5 (cont'd)

| | | | | |
|---|-----|---------|--------|---|
| <i>Paleotaxites</i> White, 1929 | 170 | 107-109 | HB, SK | Genotype by original monotypy. |
| <i>P. praecursor</i> White, 1929 | -- | 109 | HB | |
| <i>Taxites</i> Brongniart, 1828 | | | | |
| <i>T.?</i> sp. | -- | 109 | HB | |
| <i>Brachyphyllum</i> Brongniart, 1828 | | | | |
| <i>B. arizonicum</i> White, 1929 | 171 | 109-110 | HB | |
| <i>B. tenue</i> White, 1929 | 172 | 110-111 | HB, BA | |
| <i>Pagiophyllum</i> Heer, 1881 | | | | |
| <i>P. dubium</i> White, 1929 | 173 | 111-112 | HB | |
| <u>Fruits, Incertae Sedis</u> | | | | |
| <i>Cyclocarpon</i> Goepfert & Fiedler, 1857 | | | | |
| <i>C. angelicum</i> White, 1929 | 174 | 112-113 | BA | "Fruits similar to <i>Cyclocarpon angelicum</i> or that next to be figured as <i>Carpolithus</i> sp. may have been borne by <i>Supria</i> . . ." (White, 1929a, p. 112). White's final remark (p. 113), "Doubtless at some outcrop yet to be examined seeds will be abundant," remains unfulfilled. |
| <i>C. sp.</i> | -- | 113 | HB | Possibly belonging to <i>Yakia</i> , but not demonstrably so (White, 1929a). |
| <i>Carpolithus</i> ⁴ | | | | |
| <i>C. sp.</i> | -- | 113-114 | HT | Only one specimen of this form found in the collection (White, 1929a). |
| <i>Eltovaria</i> White, 1929 | | | | |
| <i>E. bursiformis</i> White, 1929 | 175 | 114-115 | HB, BA | Genotype by original monotypy. "Since the fossils here described seem to have definite configuration and characters, geographic distribution and stratigraphic significance, they should receive systematic designation" (White, 1929a, p. 115). |

¹As discussed in the text, the Hermit Shale collection has been largely unstudied since White's (1929a) monograph was published. Not included in this table is White's (1929a, pp. 41-43) new species *Rivularites permianensis* [Grand Canyon Type Fossil No. 181] from the Hermit Shale and Supai Group, which White said was a cyanophytian alga. It is, perhaps, a primary sedimentary feature, as discussed elsewhere in this paper, in the section on Paleozoic floras. Refer to Spamer (1983, 1984) for more specific collection and literature information on the type fossils listed here.

²Cf. Spamer (1983, 1984). Specific names with dashes (--) are not Grand Canyon type fossils.

³HB, Hermit Basin; HT, Hermit Trail (Hermit Basin); DS, Dripping Springs Trail (Hermit Basin); BA, Bright Angel Trail; SK, South Kaibab Trail (Yaki Trail of contemporary usage); PC, Parashant Canyon (western Grand Canyon).

⁴Andrews (1970, p. 47) remarked under the entry for *Carpolithus* Schlotheim, 1820, "Many species of fossil seeds based on impressions, compressions, and casts have been assigned to *Carpolithus* of Linnaeus and *Carpolithes* of Schlotheim. . . . *Carpolithes* is a repository for seeds and supposed seeds from almost every geological horizon that cannot be assigned to a natural plant group. . . ." Also, White (1929a, p. 114) remarked that "Similar seeds from the Permian have been described as *Cyclocarpon*."

area was an important center of botanical evolution and radiation."

AFTERWORD. To conclude this section, I would like to interject a note of historical (and paleobotanical) interest. Although David White's paleobotanical work is better known from studies in the Midcontinent region, he apparently was moved enough by the Grand Canyon to have been buried there when he died in 1935. He and his wife rest in the small, rustic cemetery at Grand Canyon Village, not far from the grand old hotel after which he named *Eltovaria*. A large metal tablet is emplaced in the rough hewn rock that serves as a headstone, and into which has been cast some of his Grand Canyon plant species. They are delightfully recognizable as three of the same specimens that appear in his 1929 monograph: *Callipteris arizonae* (pl. 13), *Supaia compacta* (pl. 15, fig. 4), and *Brongniartites? aliena* (pl. 27, fig. 2). These "metallotype" specimens may be the only such casts in existence, a fitting monument to an uncommon man and an uncommon flora.

A Note on the Grand Canyon Mesozoic Rocks

The Mesozoic strata are absent from the Grand Canyon only because they were removed by the erosional events that formed the Canyon. Just a few remnants of the Triassic strata occur very near the Canyon, and one of them is found at the brink of the chasm. Notable nearby localities, Cedar Mountain to the east and Red Butte to the south, have long been recognized as Mesozoic remnants, but no Mesozoic localities were known very near the Canyon rim until McKee (1934a, 1935c) discovered two such exposures. A small outcrop of the Moenkopi Formation is protected by the Bright Angel fault just to the southwest of Grand Canyon Village, and a somewhat larger outcrop of the Moenkopi exists west of Hance Trail (east of the village) on the lip of the Canyon. These exposures contain no fossils. Noble (1922, p. 71), however, reported logs of petrified wood in the 25-foot-thick bed of Shinarump Conglomerate (Chinle Formation) that caps Cedar Mountain.

To the north and east, within sight of the Canyon, the Vermilion and Echo Cliffs delineate the erosional receding edge of the bottom of the Colorado Plateau's great sequence of Mesozoic strata. On the plateaus of the western Grand Canyon area, these rocks again form receding cliff faces. Most of the Colorado Plateau's Mesozoic rocks are highly fossiliferous, containing remarkable assemblages of amphibians, reptiles, and mammals, and fossil floras and petrified forests. Colbert (1974) has written a brief review of this most interesting region and era.

The Anita Local Fauna (Late Pliocene?)

Twenty miles south of Grand Canyon Village, along the Grand Canyon spur from the Santa Fe Railroad's main line, fissure deposits at the former mining camp of Anita have yielded an interesting collection of fossil mammals. The first collection was made by B. C. Bicknell in 1901, and more specimens were found in 1904 by Barnum Brown of the American Museum of Natural History. Brown forwarded the whole collection to Oliver P. Hay at the U.S. National Museum, but the specimens remained undescribed until Hay (1921) included them in a study of some North American Pleistocene faunas. Hay described 15 species in 11 genera in the Anita collection, of which eight species and one genus were new. He assigned an early Pleistocene age to the collection. In 1974, Lindsay & Tessman listed the age of the Anita local fauna as early Blancan (early Pliocene). Kurtén & Anderson (1980) considered it late Blancan (late Pliocene to earliest Pleistocene), but they added that the presence of the hares *Lepus* and *Hypolagus* in the collection could indicate a still younger age of this deposit. Savage & Russell (1983, p. 364) considered the Anita locality to be among the "representative Pliocene (= Blancan, *sensu lato*) localities of

North America," placing it in the "Blancan III and IV of Repenning" (pp. 361-364) which they positioned in the late but not latest Pliocene (p. 345). These authors also altogether omitted *Lepus* from their composite Blancan fauna. For these reasons I append a question mark to the late Pliocene age of the Anita local fauna.

The fossil mammals of Anita do not in themselves represent a particularly important collection, or for that matter not even a very good one. Yet despite the mostly poor preservation, the Anita fossils in several instances have proved to be useful exercises in taxonomic identification; furthermore, they serve as the only late Pliocene(?) collection of fossils from very near the Grand Canyon. The collection is listed in Table 6.

From the Anita collection, Hay (1921) erected eight new species and a new genus on poorly preserved and, for the most part, fragmentary specimens. Of the eight species, six remain as formally valid taxa; but two of these six are questioned.

Kurtén & Anderson (1980) noted that the badger *Taxidea robusta* Hay has been found to be synonymous with *T. taxus* (Schreber), 1778. The previous nomenclature of *T. taxus* is very confusing, and *T. "robusta"* is only one of many synonyms (see particularly Rhoads, 1894, p. 524; Hall, 1936, pp. 77-83; Long, 1972; and Kurtén & Anderson, 1980, pp. 157-158).

The camel *Procamelus longurio* Hay has been declared by Webb (1974, p. 201) to be synonymous with *Hemiauchenia blancoensis* (Meade), 1945:

"* * * Hay's (1921) '*Procamelus longurio*' from Anita, Arizona, pertains to *Hemiauchenia* (see J. R. Schultz, 1938a) [*i.e.*, Schultz (1937)]. On the other hand, Hay's 'right hinder cannon bone, lacking the lower split end' must be regarded as an inadequate type specimen, as Savage (1951) and Hibbard and Dalquest (1962) have pointed out.

"Material from the Curtis ranch, Arizona, provides the most likely published record of this species in western North America. Although Gazin (1942) referred the Curtis ranch material to '*Tanupolama* cf. *T. longurio* (Hay)' in a futile attempt to salvage that trivial name, the material . . . may be compared closely with the known samples of *H. blancoensis*." [*Tanupolama* Stock, 1928.]

Schultz's (1937, p. 103) reference to "*P. longurio*" states:

". . . it is not entirely clear that the Arizona material is to be referred to *Paracamelus*. Indeed, there seems to be little reason why Hay's species should not be referred to *Tanupolama*."

Savage (1951, pp. 266-267) remarked:

"Gazin (1942) has attempted to substantiate the species *T. longurio* (Hay) from Anita, Arizona, by reference of more complete material from a stratigraphically and geographically related locality (Curtis Ranch) to this species. [But] . . . no direct comparisons could or can be made. Hay's cannon bone offers no traits worthy of a species diagnosis, and *T. longurio* should be considered a *nomen vanum*."

Savage thought that the Curtis Ranch specimen might deserve a new name. Hibbard & Dalquest (1962, p. 90) simply reiterated Gazin's diagnosis (cf. Gazin, 1942, pp. 514-517), writing, "It is impossible to assign jaw or skull elements with certainty to this species."

On the other hand, the species *Procamelus coconinensis* Hay has quite curiously been almost completely neglected. Hay (1927) reiterated *P. coconinensis* in a species list. Gazin (1942, p. 514) questioned the identification, simply remarking, "The material of the camel is very fragmentary and I am uncertain as to whether this form should be referred to *Camelops* or to the *Megatylopus-Paracamelus* group, probably the latter." No other reference to this species has appeared in the literature. Savage & Russell (1983) have noted, however, that *Procamelus* occurs in the Miocene and *Camelops* from Miocene to Pleistocene, while *Megatylopus* is found in the Miocene and Pliocene and *Paracamelus* in the Pliocene and Pleistocene; so it appears that Gazin (1942) was justified in his uncertain pronouncement. Webb (written commun., 1983) has agreed that *Procamelus coconinensis* is in need of restudy, and he confirmed that it has been virtually ignored despite the attention paid to "*P. longurio*." *P. coconinensis* should be treated as a *nomen dubium*.

Marmota arizonae Hay, a ground squirrel, has been briefly noticed by Kurtén & Anderson (1980, p. 212), who cited a 1976 personal communication from R. J. Zakrzewski that, "If the species is valid, it may be ancestral to *Marmota flaviventris*." [*M. flaviventris* (Audubon & Bachman), 1841, is a living species which does not occur in the Grand Canyon today but which has been found in the late Pleistocene faunal record of the western Grand Canyon (?23,000-?8,500 yr BP) (cf. Mead, 1981).] *M. arizonae* remains virtually unstudied.

Two species, the ground squirrel *Citellus tuitus* Hay and the hare *Brachylagus browni* Hay, have been reassigned to other genera and have been reasonably well studied. They are now *Spermophilus tuitus* (Hay) (cf. Kurtén & Anderson, 1980) and *Hypolagus browni* (Hay) Dice (1929, 1932). (The genus *Citellus* Oken, 1816, is now considered to be invalid, so it does not maintain priority over *Spermophilus* Cuvier, 1825 [cf. Kurtén & Anderson, 1980, p. 212].)

The hare *Lepus benjamini* Hay is still known only from Anita (Kurtén & Anderson, 1980). Its identification remains uncontested, although it is omitted from Savage & Russell's (1983) list of Blancan faunas.

The hyena *Chasmaporthetes ossifragus* Hay is a genus and species erected by Hay (1921) on a specimen from Anita. It is still a valid taxon even though there has been some confusion over synonyms, and some question as to whether it belongs to the Hyaenidae or the Felidae. Current paleontological literature refers the genus with confidence to the Hyaenidae.

In 1940, Stirton & Christian named a new genus and species, *Ailuraena johnstoni*, based on a late Pliocene specimen from Texas. Stirton & Christian recognized certain felid features in the premolars of their fossil, but observed that even the most primitive cats showed reduction in the premolars that are lacking in the Texas specimen; hence, Stirton & Christian referred their fossil to the Hyaenidae. T. S. Palmer subsequently communicated to Stirton & Christian that their genus *Ailuraena* was in fact preoccupied by "*Aelurina* Gill, 1871" (Stirton & Christian, 1941). They decided to instead refer "*A.*" *johnstoni* to *Chasmaporthetes* Hay, but they did so with what seems to be nebulous reasoning (Stirton & Christian, 1941):

"Although we have considered Hay's type as generically indeterminate, due to its poor preservation, it seems advisable under the circumstances to establish *Chasmaporthetes* instead of selecting a new name. We have not had the opportunity to examine Hay's type but his measurements reveal some discrepancy in the size of the two species. * * * Future discoveries may disclose the true relationship between the Pleistocene *C. ossifragus* Hay and the late Tertiary *C. johnstoni* (Stirton and Christian), when a detailed comparison of the dentitions can be made."

Furthermore, Stirton & Christian's (1940) original paper included no comparison with--nor for that matter any reference to--*Chasmaporthetes*.

The possible synonymy of *C. ossifragus* and *C. johnstoni* has been discussed, but the matter has not been satisfactorily resolved. Beaumont (1967, p. 104), Repenning (1967), Savage & Curtis (1970), Kurtén (1971), Kurtén & Anderson (1980), and Savage & Russell (1983) have treated these species as synonyms; but Galiano & Frailey (1977) and Berta (1981) considered them to be distinct species. Kurtén & Anderson (1980, p. 199, fig. 11.22) and Savage & Russell (1983, p. 363, fig. 7-8C), in regarding the species to be synonyms, went so far as to use Stirton & Christian's (1940, fig. 1) illustration of the "type" of "*A. johnstoni*" to illustrate *C. ossifragus*.

Simpson's (1945) classification of the Mammalia mentions only *Ailuraena* Stirton & Christian, without any reference to those authors' 1941 invalidation of their genus. *Ailuraena* was listed by Simpson under "?Felidae incertae sedis" (p. 121), about which he remarked (p. 230), ". . . in my opinion their fossil is doubtfully or not hyaenid." He also said (p. 231), "It certainly has remarkable resemblances to the hyenas, but it also resembles the cats and is not typically either hyaenid or felid." *Chasmaporthetes* Hay does not appear anywhere in Simpson's monograph. On the other hand, the second and third editions of Romer's *Vertebrate Paleontology* do list *Chasmaporthetes*, as a hyaenid; the second edition (1945, p. 615) as "?*Chasmaporthetes*," the third (1966, p. 383) as *Chasmaporthetes* with *Ailurena* [sic, nom. null.] as a synonym.

Kurtén (1971, pp. 206-207) clarified this hyaenid-felid conflict in the taxonomy of *Chasmaporthetes*:

"One of the most remarkable carnivores of all times was probably the hyaenid *Chasmaporthetes* These animals are found in the Villafranchian of Eurasia, the Villafranchian and mid-Pleistocene of Africa, and the Blancan of North America; this is the only hyaenid known to have invaded the New World. Although clearly a hyena in basic features, it had evolved into an extremely long-limbed, fast-running predator that shows an amazing resemblance to cheetahs both as regards to the limbs and even the teeth. To see a hyaenid playing this ecological role seems particularly incongruous."

Now as for Stirton & Christian's (1941) note on the preoccupation of *Ailuraena* by "*Aelurina* Gill, 1871," reference to Gill does not quickly clear up the problem. First, the reference is correctly Gill (1872), although within Gill's publication is a catalogue of mammalian genera that carries an 1871 date. Gill (p. 60) in turn attributed the genus *Aelurina* to Gervais, but without year of authorship. *Nomenclator Zoologicus* (Neave, 1939, vol. 1, p. 71) indicates that *Aelurina* is attributable to Gill (1872) and appends the remark, "pro *Ailurin* Gervais 1855." Referring to Gervais (1855, p. 87), there is a short discussion of the "*Félis planiceps*" (or flat-headed felids that are represented by *Felis planiceps* Vigors & Horsfield), after which Gervais summarized with the paragraph:

"Nous donnerons au groupe formé par le *Félis planiceps* le nom d'*AILURIN*."

["We will give to the group formed by the flat-headed felids the name *Ailurin*."]

Therefore, in a roundabout way we have verified, with a modest correction, that Palmer's notification to Stirton & Christian was appropriate. *Aelurina* nonetheless does not appear in the

Table 6. The Anita Local Fauna¹

| | Current Status ² | Grand Canyon Type Fossil No. ³ | Known Geologic Range ⁴ | Previous Nomenclature and Junior Synonyms; Remarks |
|--|-----------------------------|--|--------------------------------------|---|
| Mustelidae | | | | |
| <i>Taxidea taxus</i> (Schreber), 1778 | | -- | 2-11 | = <i>Taxidea robusta</i> Hay, 1921 [Grand Canyon Type Fossil No. 116] [see text] |
| Canidae | | | | |
| <i>Canis lupus</i> Linnaeus <i>nubilus</i> ? Say, 1823 | | -- | 6-11 | <i>Canis nubilus</i> ? (Hay, 1921); identification questionable |
| <i>Canis latrans</i> ? Say, 1823 | | -- | 7-11 | Identification questionable |
| Hyaenidae | | | | |
| <i>Chasmaporthetes ossifragus</i> Hay, 1921 | | 117 | 1-5 | = <i>Chasmaporthetes johnstoni</i> (Stirton & Christian), 1940 [see text] |
| Sciuridae | | | | |
| <i>Marmota arizonae</i> Hay, 1921 | | 112 | 4 | |
| <i>Spermophilus tuitus</i> (Hay), 1921 | | 113 | 4 | <i>Citellus tuitus</i> Hay; cf. Kurtén & Anderson (1980) |
| Cricetidae | | | | |
| <i>Neotoma cinerea</i> (Ord), 1815 | | -- | 10-11 | Identification questionable |
| Leporidae | | | | |
| <i>Lepus benjamini</i> Hay, 1921 | | 114 | 4 | |
| <i>Hypolagus browni</i> (Hay), 1921 | | 115 | 4 | <i>Brachylagus browni</i> Hay; Dice (1929, 1932) |
| Equidae | | | | |
| <i>Equus occidentalis</i> ? Leidy, 1865 | | -- | 6?-10 | Identification questionable |
| <i>Equus giganteus</i> ? Gidley, 1901 ⁵ | | -- | 5-10 | Identification questionable |

| | | | | |
|---|-----|----------|--|--|
| Tayassuidae | | | | |
| <i>Mylohyus?</i> sp. indet. | -- | [Note 6] | Identification questionable | |
| Camelidae | | | | |
| <i>Hemiauchenia blancoensis</i> (Meade), 1945 | --- | 2-6 | = <i>Procamelus longurio</i> Hay, 1921 [Grand Canyon Type Fossil No. 111]; Webb (1974) | |
| <i>Procamelus coconinensis</i> Hay, 1921 | 110 | -- | <i>Nomen dubium</i> | |
| Antilocapridae | | | | |
| <i>Antilocapra americana?</i> (Ord), 1815 | -- | 10-11 | Identification questionable | |

¹Cf. Hay (1921)

²As treated in this paper

³Cf. Spamer (1983, 1984); see particularly Spamer (1984, pp. 101-113) for literature histories of the type-fossil taxa. Taxa with dashes (--) are not Grand Canyon Type Fossils

⁴North America; stratigraphic range (cf. Kurtén & Anderson, 1980):

| | | |
|--|----|---------------------|
| | 11 | Holocene (Recent) |
| | 10 | Wisconsinan |
| | 9 | Sangamonian |
| | 8 | Illinoian |
| | 7 | Late Irvingtonian |
| | 6 | Middle Irvingtonian |
| | 5 | Early Irvingtonian |
| | 4 | Late Blancan |
| | 3 | Middle Blancan |
| | 2 | Early Blancan |
| | 1 | Very early Blancan |

Pleistocene

Pliocene

⁵*Equus giganteus*, sensu lato; cf. Kurtén & Anderson (1980)

⁶*Mylohyus floridanus* Kinsey, 1974, 3-4; *M. nasutus* (Leidy), 1868, 5-10

Bibliography of Fossil Vertebrates, Simpson's (1945) classification of the Mammalia, or Romer's three editions (1933, 1945, 1966).

[It should be pointed out, as a word of warning to the unindoctrinated reader, that the Greek root *aelur* (from *ailouros*, a cat; cf. Jaeger, 1944) is used within other taxonomic groups besides the mammals, lending itself to many seemingly nearly homonymous taxa. Included among the mammals is *Ailurinus* Gervais, 1870 (= *Felis planiceps* Vigors & Horsfield; cf. Hall & Kelson, 1959, vol. 2, p. 952). *Aelur* is also the root for the Infraorder Aeluroidea, into which the Felidae and Hyaenidae fall. As a matter of record, the taxonomy of all of the terrestrial carnivores, living and fossil, has traditionally been problematical (cf. Grzimek, 1975, pp. 23 ff.); but further addressing this predicament is inappropriate within the scope of this paper.]

The giant ground squirrel *Paenemarmota* Hibbard & Schultz, 1948, is interestingly almost always found in association with *Chasmaporthetes*, about which Repenning (1962, p. 555) remarked:

"It is difficult to think of these joint occurrences as coincidental in view of the great number of Blancan localities in which neither is represented. However, it is equally difficult to imagine what ecologic factor might favor the joint occurrences unless the hyaena happened to find the giant ground squirrel easy and tasty prey."

According to Repenning, the only North American Blancan hyaenid locality that lacks *Paenemarmota* is Anita. The absence of this genus there could be attributed to taphonomic loss or simply to non-collection. (Kurtén & Anderson, 1980, p. 210, remarked, "As far as is known, *Paenemarmota* is a monotypic genus." This is *P. barbouri* Hibbard & Schultz, 1948.)

The various non-type specimens in the Anita collection described by Hay (1921) were identified as the horses *Equus occidentalis*? Leidy, 1865, and *E. giganteus*? Gidley, 1901; peccary *Mylohyus*? sp. indet.; pronghorn *Antilocapra americana*? (Ord), 1815; cretoid rat, or packrat, *Neotoma cinerea* (Ord), 1815; wolf *Canis nubilus*?; and coyote *C. latrans*? Say, 1823. Hay's "*Canis nubilus*?" is *C. lupus* Linnaeus, 1758, *nubilus* Say, 1823 (cf. Miller & Kellogg, 1955). Kurtén & Anderson (1980) indicated that of these taxa only the two species of *Equus* are extinct. However, none of these taxa are found anywhere in deposits as old as the late Blancan (Kurtén & Anderson, 1980; Savage & Russell, 1983), so their identification in the Anita deposits must be questioned at this time. [If, though, Hay's generic identification of *Mylohyus* is correct, it should be noted that *M. nasutus* (Leidy), 1868, occurs only in post-Blancan deposits, while *M. floridanus* Kinsey, 1974, which Kinsey believed to be ancestral to *M. nasutus*, is presently known only from

the Blancan of Florida (Kinsey, 1974; Kurtén & Anderson, 1980; Savage & Russell, 1983).]

Late Pleistocene-Holocene Environments

Cenozoic fossils were unknown from inside the Grand Canyon until deposits in Rampart Cave were discovered by Willis Evans in the summer of 1936 while searching for archaeological and paleontologic remains in the western Grand Canyon. Since then, other caves and cloistered sites in the Canyon have yielded a remarkable collection of macro- and microvertebrates, plants, and pollen. The dry, warm climate in the Canyon has retarded the decay of these remains. The oldest material found so far is pollen which has been radiometrically dated at >40,000 yr BP (Long *et al.*, 1974). All of this fossil material is preserved in dung deposits and packrat middens.

EARLY STUDIES. Prior to the discovery of the Rampart Cave fossils, Pleistocene climates of the Grand Canyon region were interpreted (loosely) only through physiographic evidence, through fossils found in other areas, and through archaeological and dendrochronologic evidence (McKee, 1932b). Sporadic fossil finds in the Grand Canyon region teasingly pointed to a more lush, cooler environment than now exists there.

Shortly after the Rampart Cave deposits were discovered, Chester Stock and E. L. Furlong of the California Institute of Technology made a preliminary investigation that revealed some of the best preserved vertebrate remains ever found in the Southwest. The ground sloth *Nothrotheriops* (= *Nothrotherium*) was immediately recognized, although reports of a "complete mummified sloth" were obviously the exaggerated imaginations of some eager newspaper reporters (Harrington, 1936). Harrington's (1936, pp. 226-227) own description of the discoveries is quite graphic enough:

"When we entered the cool mouth of the cavern, a familiar odor struck my nostrils. It was just like Gypsum Cave [in Nevada], the unmistakable smell of ground-sloth! I have often thought the critter must have been pretty smelly for his aroma to last ten thousand years! * * * The entire floor of this large cave was composed of the dried dung of sloth, carloads and carloads of it. * * * A herd of sloths must have made it their den for years. One test hole . . . shows the deposit of dung to reach the depth of six feet in places.... The bones, hide, hair, and even a bit of the sloth's windpipe, were found in these test holes

"[The cave] . . . will yield a mass of information concerning the animals which confronted man on his entry into the Grand Cañon country, for the sloth

is not the only creature whose bones have already appeared in the test holes--there are also a mountain goat . . . , a mountain lion, and apparently a small camel."

Schenk (1937) elaborated a little more on the first examination, stating that "more than 600 bones, fragments of sloth hide with hair attached, sinews, and a portion of a trachea" had been found.

Thus began the study of the remarkable late Pleistocene record of Grand Canyon paleoenvironments.

Laudermilk & Munz (1938) presented the first scientific study of the deposits of Rampart Cave and nearby Muav Cave. Plant material had been noted in the dung deposits, which Laudermilk & Munz compared with dung deposits of Gypsum Cave. Their preliminary analysis showed that there was a "marked dissimilarity" between the plants of the Rampart-Muav and Gypsum deposits. The Gypsum Cave plants were known to have represented an environment more moist than that of today, while the Rampart-Muav plants were essentially like those now in that area. The evidence retrieved from Muav Cave, though, was considered not quite as valuable because the deposits had apparently been disturbed by Indian occupation. Laudermilk & Munz recorded 14 (questionably 16) species of plants from the Rampart dung deposits and 12 (questionably 14) species from the Muav deposits. All but three species were in common with the modern plant population.

The first comprehensive study of the Rampart Cave fauna was published as a preliminary report by Wilson (1942). Two pits had been excavated in the cave floor, from which came "several hundred determinable elements of fossil vertebrates, more than half of them of the ground sloth *Nothrotherium*" (p. 171). Wilson recorded 11 vertebrate species (including the extinct *N. shastense* (Sinclair), 1905, mountain goat *Oreamnos harringtoni* Stock, 1936, and *Equus* sp.) and some indeterminable bird remains. He noted that "the proportion of non-sloth elements increases decidedly with depth" (p. 173). On the basis of turtle and chuckwalla remains, Wilson assumed that the paleoenvironment of the cave area when these deposits were laid down was probably not much different from the present climate, although the record of *Marmota* and *Oreamnos* seemed "entirely out of place in a Lower Sonoran life zone" because they are presently found only in the much higher Transition life zone (p. 174). He did remark, however, that R. K. Grater had communicated to him an interpretation of the Rampart fauna and flora which suggested a cooler, Upper Sonoran environment with abundant vegetation. (Refer to Fig. 7, later in this paper.)

In 1946, Baldwin reviewed the progress to date in the study of the Rampart Cave deposits. Evidence of human occupation still had not been found, although only one-quarter of the cave

floor had been excavated. Remington Kellogg had made the latest excavations in 1942 under the auspices of the U.S. National Museum and with the cooperation of the National Park Service. Baldwin had taken part in that 1942 expedition, and he reported (1942, p. 95) that "numerous bones of the ground-sloth and associated mammals were uncovered," and that these remains were currently under investigation by Kellogg. By the wording of Baldwin's note, however, he apparently felt that it was only a matter of time before evidence of human occupation of the cave was uncovered. (But human remains or artifacts have never been found in Rampart Cave.)

A recent review of Rampart Cave studies to 1971 was published by Harrington (1972). This survey, with hindsight, serves as an overview of the subject just prior to the renewed and intensive investigations published in the late 1970s and early 1980s.

FAUNA. By the 1950s, records of fossil faunas began to come from other caves in the Grand Canyon, although the material from these caves was not as spectacular nor as abundant as that found in Rampart Cave. Lange (1956) reported the occurrence of the woodchuck *Marmota flaviventris* (Audubon & Bachman) from four eastern Grand Canyon caves; these are probably Holocene in age or certainly no older than Wisconsinan (latest Pleistocene), according to Lange. Also in 1956, deSaussure recorded the remains of the endangered California condor, *Gymnogyps californianus* (Shaw), from three, possibly four caves in the Canyon. Although the condor does not now range into Arizona, deSaussure noted that it may have been in Arizona as recently as historical times. On this basis, deSaussure felt that the condor remains could not be considered Pleistocene in age.

Miller (1960) reported a variety of fossil avian material, including condor, from Rampart Cave. He ascribed the highly fragmented condition of the material to "trampling by the ponderous ground sloths." This is probably a reasonable assumption because the avian fossils were deposited during the time the sloths inhabited the cave. Miller was incorrect, however, in believing that this record presented the first known occurrence of that bird in Arizona (see deSaussure, 1956). Although Martin & Guilday (1967) did not include *Gymnogyps* in their Pleistocene bestiary, Parmalee (1969, p. 206) indicated that the mountainous regions of the Southwest "probably represented the center of the bird's range since Pleistocene times until its disappearance [from this area] several hundred--or thousand?--years ago." Mead & Phillips (1981) summarized the record of condor remains in Grand Canyon caves.

Martin & Shutler (1959) published an abstract in which they reported the first comprehensive survey of the Rampart Cave paleoenvironment. Pollen retrieved from the ground sloth dung showed

that the late Wisconsinan environment (the age was determined through the first carbon-14 dating made of the Rampart material) included plants that today are found at higher altitudes and that indicator species of a warmer, drier climate appeared later. The formal results of this study were published by Martin *et al.* (1961). They presented evidence for a 25,000-yr record of discontinuous inhabitation of Rampart Cave by *Nothrotheriops shastense* (Sinclair), with the ground sloth becoming extinct there about 10,000 yr BP. Palynologic evidence indicated that an Upper Sonoran environment (cooler and wetter than the Lower Sonoran environment present at the cave today) throughout much of the time the ground sloth was present. The same indicator species are found today 2,010-3,960 ft higher in altitude. Martin *et al.*, in trying to find the cause for the ground sloth extinction at Rampart Cave, investigated the trace element nutrient content of the available plants, possible competition with other animals, and the potential effects of climatic change. But, they reported (p. 102), "Its extinction defies an obvious environmental explanation either in terms of trace element deficiency, competition, or climatic change. The cause of extinction must lie elsewhere."

In 1973, Martin proposed that the extinction of the large animals of the Southwest, including the ground sloth, was due to explosive overkill by man. Mehringer (1967) pointed out that the late Pleistocene megafauna of the Southwest inhabited the same kinds of habitats that still are present in that part of the country, and that no major barriers existed to prevent the animals from migrating to new areas as local climates changed. He agreed that man was "an important predator," but that "it seems unreasonable to support any single climatic change as the major cause of extinction" (p. 263). (The Grand Canyon did, however, present a local and decisive obstacle to cross-canyon species dispersal. Only occasionally were populations offered opportunities to cross the Canyon. This thesis will be elaborated upon in the next section, on the Grand Canyon as a biologic barrier.) The arrival in the Southwest of the paleo-Indian big-game hunters of the Clovis culture was synchronous with the extinction of the ground sloth; coincident radiometric ages of archaeological and paleontologic remains bear this out (*cf.* Long & Martin, 1974; Long *et al.*, 1974). Because paleo-Indian population dynamics was strongly influenced by major climatic events (*cf.* Irwin-Williams & Haynes, 1970), it appears that climatic change killed the ground sloths after all--indirectly.

An extension to the study by Martin *et al.* (1961) was published as a short note by Hansen & Martin (1973). There they compared modern ungulate diets in the western Grand Canyon with the diet of the ground sloth. This application of modern browsing habits to those of the late Pleistocene animals of the region seemed to indicate that significant seasonal competition among

ungulates for specific plant types may have been overlooked in the "annual" accumulations of fossil dung. A similar study of modern fecal pellets of the chuckwalla lizard was reported by Hansen (1974), in which he noted that the environment at the collection site in western Grand Canyon was similar to the paleoenvironment at the end of ground sloth inhabitation of nearby Rampart Cave. Hansen *et al.* (1976) also presented findings that imply that some non-ungulate animals could have been potential food competitors with the ungulates.

R. Hansen (1978) brought together the existing broad data base on the Shasta ground sloth food habits and the Rampart Cave paleoenvironments. (These data include some of the fossil plant studies that will be discussed in the next subsection.) His report is highly statistical and examines energy, fiber, and nutrient values. After the ground sloth food habits were compared against those of extant desert herbivores it became apparent, in a turn of scientific opinion, that *N. shastense* was not as different in its ecological role as previously believed. The digestible energy fraction of its diet was found to increase toward the time the ground sloth became extinct, so food quality and quantity were not responsible for its extinction. Hansen supported Martin's (1973) hypothesis of explosive overkill by man.

Although Rampart Cave has rightly received most of the scientific attention on the Grand Canyon Pleistocene, in recent years many other caves in the Canyon have yielded their own interesting collections of fossil fauna and flora. Lindsay & Tessman's (1974) faunal catalogue of Arizona Cenozoic localities lists only Rampart and Stanton's Caves in the Grand Canyon, the fossils of which were assigned Rancholabrean Land Mammal ages (late Pleistocene). Nearby late Pleistocene localities listed by Lindsay & Tessman are Coconino Cavern (south of the Canyon) and Cameron and Charley Day Spring (east of the Canyon), all in Coconino County. Kurtén & Anderson's (1980) monograph on the Pleistocene mammals of North America cites nine species from Rampart Cave only, but refers the reader to Lindsay & Tessman (1974) for additional localities. But many other localities are known from inside the Canyon.

Van Devender *et al.* (1977) published a survey of the late Pleistocene reptiles and small mammals of western Grand Canyon. They identified 21 taxa representing both desert and higher woodland environments. An intermixing of similarly diverse plant material was interpreted as representing a period in which there were "mild winters, cool summers, and slightly increased winter rainfall" (p. 49).

Euler (1978) presented some preliminary analyses of archaeological and paleontologic remains from Stanton's Cave, in Marble Canyon, the Grand Canyon's earliest site of human occupation (*ca.* 1100 A.D.). Radiometric ages were determined

from ten specimens; they ranged in age from 1,500 \pm to >35,000 yr BP. The late Pleistocene specimens were mostly fecal pellets. [The >35,000-yr-old specimen was a piece of driftwood that, Euler stated by referring to an unpublished report by Schleicher (1970), could have been emplaced in the cave deposits during early Wisconsinan extreme streamflow or during an episode of natural damming of the Colorado River. The dating of the driftwood was credited by Euler to Ferguson (1971). (Stanton's Cave is 144 ft above present water level.) This topic will be elaborated upon in the next section, on the Grand Canyon as a biologic barrier.] Many mammal, reptile, fish, and bird remains were noted by Euler, but he added (p. 152): "Parenthetically, in the Carnegie Museum, Pittsburgh, is a phalanx of a Pleistocene camel (*Camelops*) allegedly collected in Stanton's Cave by an amateur cave explorer." *Camelops* has since then been positively identified in the deposits of Stanton's and Vulture Caves (cf. Mead, 1981; Mead & Phillips, 1981).

Cole & Mead (1981) described the animal fractions of 53 packrat middens from eastern Grand Canyon. Dated from >27,000 to 6,800 yr BP, fossil Ptinidae and other (unidentified) insects were present in all of the middens. Of the five lizard and nine mammal species noted, only the extinct mountain goat *Oreamnos harringtoni* is absent from the Canyon today. The Grand Canyon remains of *O. harringtoni*, in fact, are so abundant in the Canyon (relative to other occurrences in western North America) that a reexamination and redescription of the species has been made possible (Mead, 1983). The extinct species is similar to, but smaller than, the living species *O. americanus*. [According to Miller & Kellogg (1955, p. 819), there are three living subspecies of *O. americanus* in North America: *O. a. americanus* (Blainville), 1816, *O. a. missoulae* Allen, 1904, and *O. a. columbiae* Hollister, 1904.] Unlike the more widespread living species, *O. harringtoni* apparently was restricted to the Great Basin-Intermountain region. According to Mead, *O. harringtoni* appears to have evolved from *O. americanus* about 100,000 yr BP, during Sangamonian time, and became extinct about 11,000 yr BP. Radiometric dating of samples from Stanton's Cave have provided youngest ages for *O. harringtoni* occupation of that site of 12,580 \pm 520 yr BP (horn sheath) and 10,870 \pm 200 yr BP (dung) (Mead, 1983). (Hester, 1960, Table 5, cited an age of 10,050 yr BP for an *O. harringtoni* specimen from Rampart Cave; and he repeated this figure in 1967, p. 184.)

Mead's (1981) paper, "The Last 30,000 Years of Faunal History Within the Grand Canyon," collates and analyzes the biotic record from nine caves and 50 packrat middens throughout the Canyon; the cave sites include Rampart, Muav, Vulture, and Stanton's Caves. He identified seven families of reptiles (21 species in 18 genera), 28 families of birds (68 species in 51 genera), and 17 families of mammals (33 species in 29 genera). Of these, six bird species and four mammal

species are extinct; two species of reptiles, two of birds, and three of mammals are not present in the Canyon today. All of these species are listed in a data matrix showing the number of specimens known from nine age ranges from 30,000 yr BP to the present. (The reader is directed to this compendium for a late Cenozoic faunal list for the Grand Canyon.) No evidence was found to indicate an abrupt faunal (or floral) change at the end of the Pleistocene. Instead, a gradual early Holocene change from woodland to desert faunal and floral communities took place; this change was complete by 8,500 yr BP.

Cole & Mayer (1982) used packrat middens and radiometric dating in a novel way: to calculate the mean rate of cliff retreat in the eastern Grand Canyon. Pleistocene middens in caves with small entrances were dated and plotted as a function of distance into the caves. Packrat activity diminishes with increasing distance into the caves, and middens are preserved until exposed by cliff retreat. Middens closer to entrances are destroyed sooner than those further into the cave and are subsequently replaced by still younger middens. The ages and spatial distribution of middens in a cave thus are diagnostic indicators of the rate of cliff retreat, according to Cole & Mayer. These authors calculated that, over a 13,000-yr period, the rate of retreat of the Red-wall Limestone in eastern Grand Canyon was 7.2-28.8 in. per 1,000 yr. (Comments were made by Hose, 1983, Haman, 1983, and Smith, 1983, but they mostly contested Cole & Mayer's method of calculating cliff retreat rates.)

The western Grand Canyon, however, has so far been paleontologically more rewarding. Cave fossil preservation has been more prevalent there; the present Lower Sonoran environment has prolonged the survival rate of the fossil materials deposited in those caves. Mead & Phillips (1981) presented a valuable comprehensive study of the late Pleistocene-Holocene fauna and flora of Vulture Cave. The Vulture Cave deposits are important because "The long temporal depth of the Vulture Cave deposits has provided the only late Wisconsinan maximum and pre-maximum plant and animal community assemblage so far reported from the Grand Canyon" (Mead & Phillips, 1981, p. 257). Furthermore, the Vulture Cave fossil record supplements well the record from such other nearby caves as Rampart and Muav; Vulture Cave has an opening that is too small to have allowed large herbivores and carnivores to enter, thus having obviated large-scale trampling of the deposits as well as having allowed skittish packrats to build middens in more open and accessible sites within the cave. Mead & Phillips identified 19 reptile, three bird, and 15 mammal taxa in Vulture Cave.

FLORA. Fauna and flora are clearly inseparable in reconstructing Pleistocene environments, but the late Pleistocene-Holocene floral story in the Grand Canyon is in itself an interesting and instructive one. Travelers in the Grand Canyon today may find it quite difficult to imagine a

juniper woodland filling the Canyon, but the paleofloral record indicates precisely that. Although the resurgence of studies of the Grand Canyon late Pleistocene is a recent (and welcome) phenomenon, the amount of data already available to researchers is overwhelming.

The first systematic approach to the analysis of late Pleistocene paleoenvironments as interpreted from Grand Canyon packrat middens was undertaken by Phillips & Van Devender (1974). Their study of the Rampart Cave area concluded (p. 119) that "differences between past and present plant communities must reflect climatic differences between the late Glacial age and the present, but what they are is very difficult to assess." The preliminary investigation of about 60 kinds of plants found in the middens suggested to these workers a 3,300-ft climatic depression of juniper and blackbrush communities during the late Pleistocene (to an altitude of 1,420 ft). Although such depressions had already been interpreted at other Southwestern localities, this was the first time that a woodland community and cooler climate had been demonstrated for the Grand Canyon's Inner Gorge.

Van Devender & Mead (1976) geographically expanded this study by comparing the late Pleistocene and modern plant communities of Shinumo Creek (eastern Grand Canyon) and Peach Springs Wash (western Grand Canyon). The plant macrofossils were extracted from packrat middens. The principal conclusion of this study was the documentation of a "xerophilous woodland as low as 735 and 860 m [2,425 and 2,840 ft] in the Grand Canyon . . . from 12,000 to 13,600 radiocarbon years ago" (p. 21). Conflicting evidence between these and other sites, however, indicated that there was no simple correlation between fossil plant assemblages and paleoclimate. This, Van Devender & Mead said (p. 21), supported "the hypothesis that plant species responded to changing environments in an individualistic manner (Gleason, 1939) rather than plant communities being depressed as units." This theme would continue to show up in later studies of the Grand Canyon late Pleistocene.

Phillips (1977, 1978) identified four stages of plant community dominance in the western Grand Canyon, from 8,500 yr to at least 30,000 yr BP: 30,000-24,000 yr BP, an interstadial mixture of woodland and desert species dominated by junipers; 24,000-14,000 yr BP, full glacial, the most mesophytic of the stages; 14,000-11,000 yr BP, some desert species begin to return; and 11,000-8,500 yr BP, woodland species gradually disappear and the single-leaf ash overtakes the junipers.

Euler's (1978) preliminary investigation of the Stanton's Cave deposits yielded a variety of paleobotanical material. Some initial correlations were then made with better-studied sites in western Grand Canyon and elsewhere in the Southwest. The significance of this material and the fossil fauna of the cave, Euler stated, still must undergo more rigorous examination before any

firm conclusions can be drawn. Euler concluded, though, that Stanton's Cave is an important site for paleoenvironmental studies.

The Grand Canyon studies soon began to fit into the evolving picture of Southwestern Pleistocene-Holocene climates. Martin & Mehringer (1965), Van Devender (1977), Brakenridge (1978), Van Devender & Spaulding (1979), Galloway (1983), and Spaulding (1983) appraised the evidence for late Pleistocene-Holocene woodlands in the Southwestern deserts (which includes the Inner Gorge of the Grand Canyon). Martin & Mehringer's (1965) paleobiogeographical review of Pleistocene palynology in the Southwest included the 1961 Rampart Cave study by Martin *et al.* as the sole Grand Canyon reference. But Martin & Mehringer included a map of the distribution of full-glacial vegetation of the Southwest 17,000-23,000 yr BP (their fig. 4) that illustrates the important climatic barrier represented by the Grand Canyon. (This will be of more significance in the section of this paper on the Grand Canyon as a biologic barrier.) Yet changes in climate have greatly affected the distribution of vegetational communities in both time and space. In comparing the shift from pluvial to nonpluvial, nonglacial climates throughout North America, Van Devender (1977) explained the Southwest's ~4,000-yr tardiness in shifting as the lingering effect of melting continental glaciers on general patterns of atmospheric circulation. After 8,000 yr BP, the transition to wholly desert environments was complete.

Brakenridge's (1978) study of the full-glacial period from 27,000 to 13,000 yr BP in the Southwest led him to believe that this period, although clearly cooler and more luxuriant than the present desert environment, was not necessarily a wetter period. He plotted the orographic snowline of the Southwest to be 3,300 ft lower than today's snowline and calculated the annual average temperature to be 7°-8° C cooler than today. This cooler climate, together with lowered evaporation rates of the Southwestern pluvial lakes and increased moisture retention of soils, would have allowed a coniferous woodland to grow ~2,300 ft lower into the deserts. Galloway (1983) sustained a dry full-glacial-climate interpretation for the late Wisconsinan Southwest, one some 10° C cooler than present levels. He indicated that the latest Wisconsinan Southwest could have had a "mild-pluvial" climate.

Van Devender & Spaulding (1979) expanded the study of the Southwest's late Pleistocene climate to 22,000 yr BP. Juniper-pinyon woodland communities were found to have been present throughout most of the Southwestern deserts during late Wisconsinan time (22,000-11,000 yr BP), although, as previously reported by Van Devender & Mead (1976), pinyon was absent from the community in western Grand Canyon. The hypothesis of differential plant species response to climatic change remained valid in Van Devender & Spaulding's work, but they stated that the overall response

to the changing climate 8,000 yr BP was quick. This interpretation, in retrospect, contrasts with others which suggest that changes in floral communities were gradual (*e.g.*, Mead, 1981). Spaulding (1983) indicated further that although late Pleistocene-Holocene xerophytic conifer woodlands were widespread in the Southwest at that time, extensive desert vegetation *did* begin to develop before the middle Holocene.

The Vulture Cave study by Mead & Phillips (1981) examined fossil packrat middens as old as 30,000 yr BP. Of 47 plant taxa identified from 14 middens and from one sedimentary unit (11,830-22,720 yr BP), 14 were extralocal species no longer present in the area, 16 were relict species, 19 were still indigenous to the area, and eight were annuals. Only 28 percent of the species no longer occur in the area, but "Some of the species consistently found together in the late Pleistocene middens grow together today only in exceptional microhabitats" (Mead & Phillips, 1981, p. 284). No species were new identifications in the fossil flora community of the area.

Cole (1978, 1981, 1982) published the first systematic examination of vegetational paleogradient in the eastern Grand Canyon. Fifty-three packrat middens yielded radiocarbon ages from 34,300 to <100 yr BP; they were from altitudes between 3,135 and 7,260 ft, nearly the entire depth of the eastern Grand Canyon, representing all present life zones. Fossil plant material from these middens indicated five definable climatic periods: full glacial (21,000-15,800 yr BP), during which the Utah juniper (presently occurring within 1,650 ft of the Canyon rim) was depressed to the Canyon bottom; late glacial (15,000-11,000 yr BP), with reduced climatic extremes; early Holocene (11,000-8,000 yr BP), when many modern dominant species began to appear; mid-Holocene (8,470-6,800 yr BP), when hot and/or dry conditions prevailed; and late Holocene (<2,300 yr BP), when plant communities were qualitatively and quantitatively identical to today's communities. Cole concluded that simple altitudinal displacements of life zones cannot account for the observed distributions of fossil and modern plant species. He proposed a model in which latitudinal shifts in climate also influenced the distributions of individual species. The overall association of fossil plants of the eastern Grand Canyon most resembles modern associations 280 miles to the north of the Canyon, according to Cole.

In an unpublished preliminary report, Behrens-meyer *et al.* (1982) described a reconnaissance of potential late Cenozoic deposits in the Grand Canyon. Among the objectives of that survey was a search for late Pleistocene fossils. A particularly promising locality is a closed sedimentary basin at Surprise Valley. Weber (1982) presented an appendix to this report, describing a palynological study of eight soil samples and one packrat midden, all of "probable Pleistocene age," from three localities; the midden and one soil

sample were from Surprise Valley. Five soil samples, including the one from Surprise Valley, yielded no pollen, but 28 plant taxa were identified in the midden, all 28 of which are modern species. Weber also remarked that the midden should be radiometrically dated. The three soil samples that contained pollen had only a few mostly unidentifiable pollen grains, not enough for a statistically reliable sample.

AFTERWORD. Rampart Cave is not only the most scientifically valuable of the Grand Canyon late Pleistocene deposits, but is an important world locality, too. Soon after its discovery in 1936, the National Park Service installed a gate at the cave entrance to bar entry by inquisitive persons who might disturb the deposits. Grater (1958, p. 32) remarked on this: "Because of its great research value, the cave is closed to entry today by a steel door [gate], placed there by the National Park Service to protect its still unexcavated portions from possible loss through unauthorized digging or from a carelessly dropped match or cigarette." His remark was sadly prophetic.

In July, 1976, a fire was discovered in Rampart Cave (see Priehs, 1976). Park Service rangers theorized that vandals had climbed to the cave entrance, broken the padlock, and entered with homemade torches for illumination. One torch carelessly left behind started a slowly smoldering fire that defied almost all efforts to extinguish it. Soon after the fire was discovered, the Park Service sealed the entrance to cut off the oxygen supply; but the fire continued, fed by air through an unknown vent or by trapped oxygen within the dung. Nearly a year later, the fire still burned (Anonymous, 1977).

When the cave was reopened, part of the roof was found to have collapsed, weakened and cracked by the heat, and the Federal Mining Enforcement and Safety Administration was called in to build supports. Once the cave was made safer, helicopters lifted huge containers of water from the river to the cave, eventually quenching the stubborn fire. Paul Martin, who for more than 20 years had studied the Rampart Cave deposits, returned to the cave and observed that more than half of the cave's contents had been destroyed, including all of what he called "the best stratified material" (Blair, 1980).

The Grand Canyon As a Modern Biologic Barrier: An Aid to Evolution?

A foreboding physiographic feature, the Grand Canyon has for centuries been an obstacle to human travel. To the casual observer, the Canyon must also be a decisive barrier to animal migration; if so, there must be different kinds of animals on opposite sides of the gulf. This is partly true: the Canyon is a transverse barrier to non-flying animals of the adjacent plateaus, but it is also a natural corridor for animal mi-

gration through the length of the Canyon. Animals can enter from either end, particularly from the western end of the Canyon at the Grand Wash Cliffs where it opens to the semi-arid Basin and Range province. The desert climate of the Inner Canyon is an extension of the desert to the west. Plants and birds, of course, are relatively oblivious to the Grand Canyon barrier; they require only the appropriate ecological conditions for the survival of their kinds. Also, along the Colorado River corridor there are riparian communities of plants and animals.

Most animal and plant species are restricted to specific ranges of altitude that are ecologically controlled by climate. These life zones have been studied in the Grand Canyon area ever since Merriam's (1890) pioneering ecological survey of the area between the Canyon and the San Francisco Mountains to the south; in fact, it was that study which was the first to present the concept of stratified life zones. The area between the Grand Canyon and the San Francisco Mountains is the classic case study in altitudinal influences on life zones (see Fig. 7). Within 60 miles, altitudes here range from 2,500 ft at the Colorado River to 12,633 ft at Mount Humphrey (which also is the highest point in Arizona). The fauna and flora of this area change so dramatically as one ascends that, to see the same changes at or about sea level, one has to travel from northern Mexico nearly to Hudson Bay. Almost as dramatic are the life zone changes in the 20 horizontal miles between the Colorado River and the summit of the Kaibab Plateau to the north, a rise from 2,500 ft to 9,250 ft.

In the Grand Canyon, the life zones are particularly well defined on the steep canyon walls. The life zones can be mapped as bands roughly paralleling the topographic contours. Although the divisions between these zones in the Canyon are sharp, they do not quite coincide with the variations in climate. This enigma was recognized by Coville & MacDougal (1903, p. 23), who suggested that storms, developing on the surrounding plateaus, cross over the Canyon and deliver more water to the semi-arid Inner Canyon than would normally be received there. This condition is not duplicated in the flat semi-arid deserts of the region. Lateral zonation is evident, too, effected by the seasonal distribution of precipitation (Jameson, 1969), although the lateral gradients are not sharp like the vertical ones.

Many species are seen to be isolated in climatic benches along the Canyon walls. But the Grand Canyon life zones have not been static; in the past, climatic variations alternately depressed and raised them in elevation. Opportunities arose for animal species to cross the Canyon when particular zones extended to river level. Throughout the Pleistocene, local and regional fluctuations in climate must have affected runoff and streamflow; this also affected animal migration across the Canyon. During times of very high streamflow, the Colorado River must have

been an imposing spectacle. Hoffmeister (1971, p. 29) presented an interesting thought on cross-canyon animal migration at such times:

"Even though some species were able to move down the canyon, they now found the river to be a formidable barrier. Perhaps if forests grew along the river's edge, there would be an increased likelihood that some trees, when washed out, might raft animals from one side to the other."

"Forests" did not exist in the Grand Canyon near river level, at least not during the late Pleistocene. Driftwood logs are not unusual, however, and during periods of extreme runoff there probably was much more flotsam washed down from forested tributaries upstream. But, such speculation aside, Hoffmeister's suggestion is improbable. Very high water flow through the Canyon *may* have been slow enough at the surface to allow this to happen, across pools before any rapids were encountered. Fortuitous rafting as a mechanism for species dispersal across the Canyon presumes that enough surefooted individuals of both sexes made the crossing frequently enough and geographically close enough to establish breeding populations on the other side.

A more plausible mode of cross-canyon dispersal would take place at times of episodic damming of the Colorado. Schleicher's (1970; *vide* Euler, 1978) record of late Pleistocene (>35,000 yr BP) driftwood in Stanton's Cave (see the section on late Pleistocene environments) lends credibility to the idea of temporary ponding of the river. That piece of driftwood had to have been emplaced in the cave, 144 ft above present river level, by an episode of extraordinarily high water. As Schleicher suggested, such high water might have been the result of (a) ponding behind dams built by catastrophic debris flows from major tributary canyons, or behind lava dams built in western Grand Canyon, or (b) extreme streamflow of a through-flowing Colorado river. But if extreme streamflow was the case, a volume of >10,000,000 cubic feet per second (cfs) would have been necessary for the river to flood Stanton's Cave (Euler, 1978, p. 156, citing a 1971 personal communication from M. E. Cooley). (The record modern Colorado River flood in the Grand Canyon was measured at <500,000 cfs.) The ten million figure is heart-stopping even by Pleistocene standards unless it can be attributed to a hydrologic (glacial?) catastrophe in the upper Colorado drainage basin. The hypothesis of damming is more conservative.

Lake-forming by damming is a well documented phenomenon around the world in both the present and the geologic record. (See Hutchinson, 1957, for classifications of modern lake types.) In the Grand Canyon, two types of lakes may have been formed; these can be classified to Hutchinson's Type 19a (lake formed by lava flow damming of a valley) and Type 20 (lake held by landslide damming).

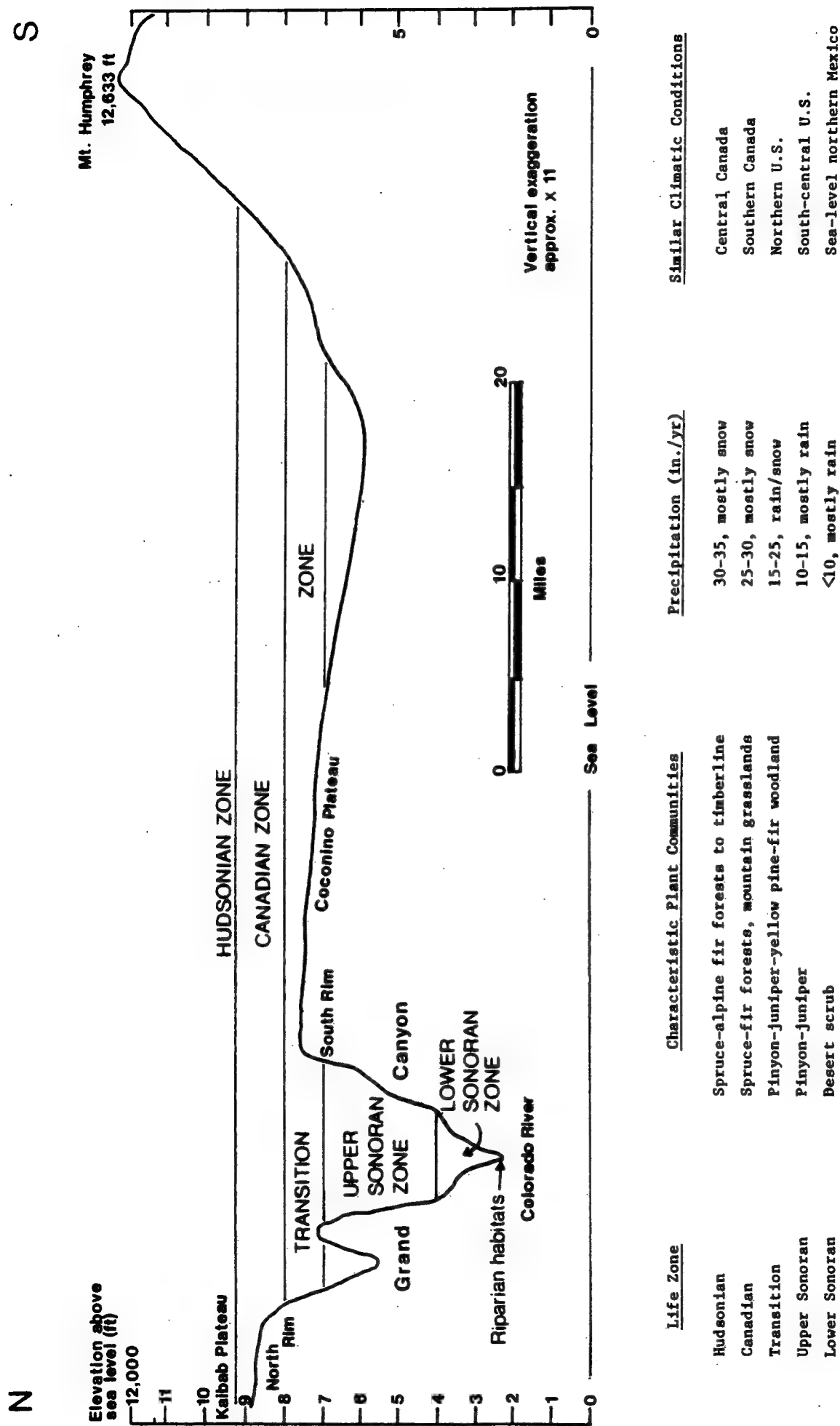


Figure 7. Recent (Mid- to Late-Holocene) Life Zones of the Grand Canyon Region. Late Pleistocene climatic variations resulted in depression of life zones to lower elevations during cooler climatic episodes. Whether some episodes also represented wetter periods is a matter of discussion among researchers of the Pleistocene Southwest.

Catastrophic debris flows in the Grand Canyon are fact; the last one occurred in December, 1966, after an unusually severe storm over the Kaibab Plateau (Cooley *et al.*, 1977). The historic flows were not so catastrophic as to dam the Colorado; but the late Pleistocene events, through inference from documented pluvial paleoclimatic conditions, probably frequently overwhelmed the historic flows in both volume and intensity. A dam that completely blocked the river would provide an empty river bed downstream for animals to wander across, as well as itself being a route across the river. Dam overflow or collapse probably quickly ensued, after which animals would again be isolated. Nonetheless, just a few days would be all the time necessary to let some individuals wander across the river while foraging, and by happenstance be cut off from returning by resumption of streamflow. It seems reasonable that some large blockages could have remained intact for many months, too, depending on streamflow and the structural integrity of the dam.

Although there is no positive evidence of a debris dam on the Colorado in the Grand Canyon, Euler (1978, p. 158) noted "that geologists from the U.S. Geological Survey discovered what may be evidence of landslide damming of the Colorado River at the mouth of Nankoweap Creek, approximately 32 kilometers [20 miles] downstream from Stanton's Cave." If this can be verified, very-large-scale debris damming of the Colorado will have to be viewed as an active agency in intracanyon species dispersal. (In deference to Hoffmeister, some animals could have been rafted across the backdam lake, too.)

River damming is positively known to have occurred in western Grand Canyon. Lava flows cascaded into the Inner Gorge near Toroweap many times during the late Cenozoic. Stratigraphically identical remnants of some flows are found on both sides of the gorge (see McKee & Schenk, 1942; Hamblin, 1969, 1970, 1974), and some of these cascades, long since cut through by the river, therefore blocked the gorge. The obvious consequence is ponding of the river. (See Redfern, 1980, pp. 108-109, for a photographic/artistic reconstruction of one such damming event.) The higher dams must have created large lakes in central and eastern Grand Canyon. Schleicher (1970; *vide* Euler, 1978, p. 156) pointed out that "Hamblin's 'F' flow has remnants at an elevation of 3100 ft (about 100 ft higher than Stanton's Cave)." This means that a lake backed up through central Grand Canyon, through eastern Grand Canyon's Inner Gorge and Nankoweap area, and reached well up Marble Canyon virtually to Lees Ferry. The steep canyon walls throughout most of the lake's reach, however, restricted the lateral expansion of the lake, particularly in its upper reaches, except in tributary canyons.

The Colorado River has cut through all of the Toroweap lava flows. The lowest flow, just 50 ft above present river level, has been radiometri-

cally dated at ~1.2 m.y. old (McKee *et al.*, 1968). This means that the Colorado had already cut to within 50 ft of its present depth ~1.2 m.y. ago. So the Grand Canyon clearly was a major physical barrier throughout Pleistocene time.

Lava dams probably survive much longer than debris dams; they are inherently structurally more sound and less liable to collapse by backdam water pressure. Each damming episode by the intracanyon lavas of Toroweap refilled the lake behind them; each time the river may have taken years to fill the lake. This was ample time for animals to migrate across the Canyon, and for populations to interbreed before streamflow resumed past the dam. Of course, the intervals between successive damming events may have been long. The Grand Canyon has therefore been an effective barrier in the late Cenozoic, permitting only rare incidents of cross-canyon migration while intermittent Lake Balquidder* was being refilled.

Stanton's Cave could become a control site for future studies of Grand Canyon areas suspected of having been inundated. The cave may well have been flooded by Lake Balquidder (at least once) and it may have been flooded by a lake behind a debris dam at Nankoweap Creek. The geomorphology, sedimentology, and paleontology of the cave de-

*In June, 1871, during the second Colorado River expedition, John Wesley Powell entertained his fellow explorers with readings from Sir Walter Scott's romantic poem, *The Lady of the Lake* (*cf.* Dellenbaugh, 1908, p. 31). Through allusion to the title, and in keeping with the custom of naming some of the Grand Canyon's geographic features after inspiring literary figures and places, I informally refer to the intermittent lava-dammed Grand Canyon lake as Lake Balquidder. The name is that of a Scottish district, mentioned in *The Lady of the Lake* in a delightfully appropriate passage:

*Not faster o'er thy heathery braes,
Balquidder, speeds the midnight blaze,
Rushing, in conflagration strong,
Thy deep ravines and dells along,
Wrapping thy cliffs in purple glow,
And reddening the dark lakes below . . .*

- Canto III, xxiv, 1-6

Sir Walter explained in "Notes to Canto Third" (*cf.* Scott, 1836, p. 193; a shirt-pocket American edition perhaps like the one Powell carried down the Colorado) that the passage refers to heaths on the moors of Balquidder set afire to burn off older, tough plants to make room for more suitable "young herbage" for sheep. He remarked, "This custom . . . produces occasionally the most beautiful nocturnal appearances, similar almost to the discharge of a volcano."

Powell (1875, p. 95) immediately recognized the intracanyon lavas during his first river trip, in 1869. His thoughts on the conflagration there are most graphic, as inspired as the passage about the fires of Balquidder:

"What a conflict of water and fire there must have been here! Just imagine a river of molten rock, running down into a river of melted snow. What a seething and boiling of the waters; what clouds of steam rolled into the heavens!"

posits and the area near the cave will have to be closely examined before any further conjecture can be presented.

Despite cross-canyon migration of selected species during damming events, populations of one species, separated by the river, could remain segregated long enough for genetic variants in either population to dominate (if ecologically warranted and successful). Such isolation is certain when the life zone at river level rises in elevation in response to climatic warming or changes in precipitation patterns. The elevated life zone thus becomes a life zone bench on either wall of the Canyon; later damming events have no effect on the broken line of communication between the populations of that zone.

The concept of stranded species at the Grand Canyon is not new. In 1937, H. A. Anthony, Curator of Mammalogy in the American Museum of Natural History, mounted a major expedition to an isolated outlier of the Grand Canyon's North Rim, Shiva Temple. The expedition was to determine whether species, ostensibly cut off from the rest of the world since the last Ice Age, had evolved into new forms. Shiva Temple is separated from the North Rim by a steep, narrow, presumably "impassable" topographic saddle thought to have been made during the Ice Age. Such a novel idea as an isolated community of animals was quickly picked up by the press. The Shiva "sky island" was soon sensationalized as a real Lost World, and the exploits of the scientist-mountaineers were closely followed (e.g., *New York Times*, 1937). Alas, not only were there no fabulous creatures atop Shiva, but deer and other animals were found to have regularly made their surefooted ways across the precipitous saddle. The explorers also found American Indian relics on the butte.

Lost worlds notwithstanding, the Grand Canyon is at least old enough to have permitted physical segregation of different communities of single species. As noted above, the Colorado River had cut to within 50 ft of its present depth by ~1.2 m.y. ago, as indicated by radiometrically dated lava flows incised by the river in western Grand Canyon (McKee *et al.*, 1968). This is a minimum age, and the time frame of the Grand Canyon barrier can of course be extended further; ample time, probably, to allow genetic variants to become established. But from this period of time no fossil evidence has yet been found that could positively indicate evolutionary radiation.

Evolution, as observed in the fossil record, can be attributed to a number of environmental and genetic effects, all of which of course are matters of controversy. On small intracontinental scales, exogenic effects on evolution are not well defined. Is the Grand Canyon (which bisects a largely temperate biotic island in turn bounded by semi-arid deserts) both old and topographically decisive enough to instigate divergent evolution?

That the Grand Canyon is a transverse biologic barrier is demonstrated by many examples.

To cite a few: the Arizona tiger salamander, *Ambystoma tigrinum nebulosum* Halowell, is restricted to the area south of the Canyon, while the Utah tiger salamander, *A. t. utahensis* Lowe, is restricted to the north of the Canyon (Miller *et al.*, 1982); some species of ants are apparently segregated in life zones on one side of the Canyon (Wheeler, 1906), as are some species of terrestrial molluscs (Pilsbry & Ferris, 1911); and many mammal species are isolated from closely related species on opposite sides of the chasm (Cockrum, 1960; Hoffmeister, 1971).

As a lateral conduit, the Grand Canyon again hosts many examples. For instance, the subspecies of Canadian beaver *Castor canadensis repentinus* Goldman is found along waterways in the deserts west of the Canyon as well as in the Canyon upstream along the Colorado, and part way upstream along the Little Colorado River into the Painted Desert; the canyon mouse, *Peromyscus crinitus stephensi* Mearns, is found in western Arizona and in most of western Grand Canyon, while *P. c. auripectus* (Allen) is found in central and eastern Grand Canyon and in all of northeastern Arizona; and the Grand Canyon and the Little Colorado drainage form part of a donut-shaped area of Arizona in which the raccoon *Procyon lotor pallidus* Merriam is found (Cockrum, 1960).

Still other animal species are known only from inside the Grand Canyon; for example, the Grand Canyon rattlesnake, *Crotalus viridis abyssus* Klauber, a remarkable light brown and vermilion-to-salmon pink rattler that appears to have developed its unusual coloring as a defensive adaptation in a land painted with red hues. In contrast, the Great Basin rattlesnake, *C. v. lutosus* Klauber, is known only north of the Canyon; the Hopi rattlesnake, *C. v. muntius* Klauber, is found only south of the Canyon (Miller *et al.*, 1982).

Peck (1980) presented an interesting case for the environmental stranding of cave invertebrates in the Grand Canyon. As already noted, spruce-fir montane forest communities extended into the Canyon during part of late Pleistocene time. Invertebrates inhabiting the forest litter also must have moved into the Canyon. But during subsequent retreat of the life zones to higher altitudes, some of these animals continued to inhabit the caves into which they have moved during the late Pleistocene, and wherein they still live. (All of the caves examined by Peck are in the eastern Grand Canyon.)

The most-cited case study of isolated Grand Canyon species is that of the tassel-eared squirrels, the subgenus *Otosciurus* Nelson, 1899 (genus *Sciurus* Linnaeus, 1758). The two members of *Otosciurus* are the Abert squirrel (*Sciurus aberti* Woodhouse, 1854; the type species of *Otosciurus*, cf. Walker *et al.*, 1975) and the Kaibab squirrel (*S. kaibabensis* Merriam, 1904). These squirrels are so remarkably alike, and yet definitely segregated by the Canyon, that they appear to be

living examples of evolution at work. They are the same in size and proportion, and they are predominantly grey to bluish grey, with the middle of the back reddish. But the Abert squirrel has white underparts, including the underside of the tail, while the Kaibab squirrel has black or dark grey underparts and a wholly white tail. It appears that the Kaibab squirrel's coloring befits its special environment on the Kaibab Plateau, where very heavy snows accumulate during a long winter season. In Arizona, the Abert squirrel is found in a crescent-shaped zone of higher elevation from the South Rim of the Grand Canyon on into west-central New Mexico; but the Kaibab squirrel is unique to the Kaibab Plateau (Cockrum, 1960). The two squirrels are separated only by the gulf of the Canyon, and the Kaibab squirrel has no natural route off of the Kaibab Plateau. Other subspecies of *S. aberti* occur in Colorado, New Mexico, Arizona, and northern Mexico. All of the tassel-eared squirrels are found in close association with stands of the Ponderosa pine, *Pinus ponderosa* (Merriam, 1890 [cf. *S. aberti*]; Keith, 1965).

Because of the remarkable similarities between the Abert and Kaibab squirrels, there is some question as to whether they represent truly distinct species. Although various workers have subdivided the *S. aberti* group into several subspecies (eight are listed by Nash & Seaman, 1977), *S. kaibabensis* has traditionally been retained as a separate species, almost always with remarks on its similarity to *S. aberti* (Merriam, 1904; Goldman, 1928; Pratt, 1935; McKee, 1935b, 1941; Howell, 1938; Miller & Kellogg, 1955; Hall & Kelson, 1959; Hoffmeister, 1971; Walker *et al.*, 1975, vol. 2, pp. 671-672; Nash & Seaman, 1977; Whitney, 1982). Rasmussen (1941), in his ecological monograph on the Kaibab Plateau, treated *S. kaibabensis* as a distinct species without comparison to *S. aberti*. Burton (1962) regarded the Kaibab squirrel as a "distinct form" of *S. aberti*, and Patton *et al.* (1976) considered the Abert and Kaibab squirrels both to be subspecies (*S. a. aberti* and *S. a. kaibabensis*). But specific and subspecific pigeon-holing can be potentially misleading because of genetic variants within a given group; for example, Ramey & Nash (1976b) have observed genetic polymorphism in coat color within *S. a. ferreus* of north-central Colorado.

If *S. aberti* and *S. kaibabensis* are indeed distinct species, they are so only marginally. McKee (1941) remarked that even within these two groups characteristics of one species occasionally show up in the other. He concluded (p. 20):

"... we appear to have in the Tassel-eared Squirrels a fine example of evolution in its first stages, not yet well defined in its trends and not yet in operation for a very long period, but having definite opportunities to develop well-isolated forms along independent lines."

Ramey & Nash (1976a), however, refuted McKee's observation of an interspecific geographic cline in squirrel size, decreasing from Arizona to Colorado. But, regardless of taxonomic fine-tuning by some researchers, the evidence in *S. kaibabensis* of an isolated, unique group of animals is incontrovertible. To many of us, what we observe in the Kaibab-Abert squirrel disparity is what we expect--or hope--to see in evolutionary divergence. We have at hand an empirical test of the hypothesis.

Pseudofossils

Pseudofossils might not normally warrant discussion in a paleontological paper, but the Grand Canyon strata have yielded a variety of interesting and occasionally controversial forms, including two "holotypes."

RIVULARITES FLICHE. The first of the "holotypes" is "*Rivularites permiensis*" White. The species was described by White (1929a) as an alga, but *Rivularites* Fliche, 1906, has since been declared by most workers to be inorganic (see the section on Paleozoic floras). As already noted, however, *Rivularites* continues to be reported from the Grand Canyon strata as algal remains (cf. McKee, 1982), and its identification as such appears to be paleoecologically appropriate.

"BROOKSELLA CANYONENSIS" BASSLER. The second Grand Canyon pseudofossil "holotype" is remarkable for the academic excitement it generated. This is "*Brooksella canyonensis*" Bassler, 1941, the Grand Canyon jellyfish. Discovered in 1934 by C. E. Van Gundy in the late Precambrian Nankoweap Formation of eastern Grand Canyon, the then-unique fossil was immediately celebrated as a true Precambrian jellyfish (e.g., Van Gundy, 1937; Hinds, 1938; Carnegie Institution of Washington, 1938), and it may even have led Hinds (1940) to provisionally raise the whole Grand Canyon Supergroup into the lowermost Paleozoic. It is disappointing that Charles D. Walcott, who had died just a decade before, did not find this fossil during his own explorations in this area of the Canyon. (Ironically, Bassler, 1941, determined that the jellyfish belonged to one of Walcott's Paleozoic genera, *Brooksella* Walcott, 1896.)

Although some members of the academic community confidently placed the jellyfish in the realm of true fossils, Bassler (1941) formally named the fossil with reservation; he acknowledged that it could be an inorganic feature. But the organic nature of the fossil was not really questioned until the 1960s. Most workers (see particularly Cloud, 1960, 1968) now regard the medusoid impression as definitely inorganic. It is, perhaps, a gas blister or a compaction feature that surrounded a soluble object (Cloud, 1960, 1968). This pseudofossil has also been identified from other world localities and from above the Precambrian (Häntzschel, 1975), including a partial second specimen from the type locality (Cloud, 1968).

"*B. canyonensis*" drifted slowly through the academian swamps of taxonomy; its "certain" medusoid identification was perpetuated for a quarter century (Van Gundy, 1937a,b, 1951; Bassler, 1941; Howell, 1956; Harrington & Moore, 1956). Seilacher (1953, p. 430; 1956, pp. 158, 166), however, felt that the Grand Canyon jellyfish could in fact be a star-like burrow of a filter-feeding benthonic worm—a trace fossil. Although he did not mention "*B. canyonensis*" by name, Seilacher (1956) did place the word "Medusen" within quotation marks. Glaessner (1962, pp. 479, 484), while taking note of Cloud's (1960) inorganic interpretation, declared that the fossil could be "matched perfectly" with elements of the late Precambrian Ediacara fauna of central Australia; and Glaessner placed the genus name within quotation marks. Cloud's compaction feature interpretation was later wholly refuted by Glaessner (1969), who, likening the fossil to a burrowing trace made by an annelid worm, reclassified it as *Asterosoma? canyonensis*. As a point of interest, Seilacher (1969) placed *Asterosoma* von Otto, 1854, as an element of the *Cruziana* ichnofacies of bathymetric zonation (see the section on Paleozoic trace fossils regarding this ichnofacies). Although therefore paleoecologically compatible with *Brooksella*, the ichnogenus *Asterosoma* is so broadly defined (cf. Häntzschel, 1975) that Glaessner's reclassification seems almost superfluous, save that it removed "*B. canyonensis*" from the medusae. However, the existence of Precambrian medusae in the Grand Canyon remains unproven (see the next subsection, on "Other Medusae").

Kauffman & Steidtmann (1981, pp. 924-925) quickly reviewed the nomenclatural and paleobiological reassignments of "*B. canyonensis*" and concluded with the remark that "subsequent examination of this structure by Kauffman (ms. in preparation) supports this interpretation [*i.e.*, Glaessner's annelid worm trace fossil]" (p. 925). Soon thereafter, Kauffman & Steidtmann (1983) and Kauffman & Fursich (1983) reinterpreted "*B. canyonensis*" as a complex metazoan trace fossil. With regard to Precambrian trace fossils generally, these investigators inferred from a variety of sedimentologic and paleobiologic evidence that vertical-burrowing metazoans appeared before the horizontal-burrowers. Hence, the assertion was made that a more gradual radiation of the vertical-burrowers began at a time earlier than previously believed. However, Kauffman & Steidtmann (1983, p. 620) in effect negated the hypothesis by appending the remark, "In reality, the Precambrian and basal Cambrian trace-fossil record is too sparse and localized to make such interpretations." The problem of "*B. canyonensis*" remains unresolved, although certainly no less interesting.

OTHER "MEDUSAE." Other "medusoids" from the Grand Canyon have turned up at the Hakatai Shale-Bass Limestone boundary (late Precambrian Unkar Group) near South Kaibab Trail. Seilacher (1956)

discussed depressions that are surrounded by concentric wrinkles; these he called "diagenetic haloes around crystal pseudomorphs" (Ford & Breed, 1977, p. 173), but Alf (1959), from a new collection from the same locality, called these features jellyfish impressions. Cloud (1960, 1968) countered with the observation that some of the impressions resembled raindrop pits, while others appeared to be gas-evasion structures. Cloud (1960, p. 43, in a footnote added in proof) unilaterally called Alf's and similar specimens "gas blisters or their impressions." In 1968, though, Cloud again cited the raindrop/gas blister interpretations without comment on his 1960 footnote. Glaessner (1966, 1969) believed that Alf's first jellyfish-like structure was an algal feature, but Nitecki (1971) noted that this and similar features contained no organic morphologic structures. Nitecki treated Alf's second jellyfish as a concretion. Ford & Breed (1977, p. 173) confidently summarized that, in any case, "the existence of fossil jellyfish in the Grand Canyon must be regarded as unproven."

OTHER PSEUDOFOSFILLS. Jellyfish notwithstanding, Alf (1959) also called attention to "vermiform markings" and a "silicified sponge" from his Hakatai-Bass locality. The late Precambrian presumed worm traces have been recognized by other investigators as desiccation features in mud. A precedent for such an interpretation in the Unkar Group was established more than 50 years ago by McKee (1932a), who observed mud-crack "fucoids" in the Dox Formation. Cloud (1968) called Alf's sponge a nodule, and no researchers have since thought otherwise. Nitecki (1971) discovered similar siliceous concretions in the Bass Limestone (at a locality 20 miles downstream from Alf's locality), pronouncing them inorganic. But Nitecki also observed that these concretions, when dissolved in hydrofluoric acid, released tiny "pollen-like round bodies" that are similar to Downie's (1969) organic residue. Ford & Breed (1977) said that these could be nanoplankton that require future investigation. Such investigation, however, is still awaited; so the nature of these concretions is at best uncertain. Nitecki also discovered "branching structures" that he called "very interesting . . . even if most puzzling" (p. 8). He continued, "The branches are . . . reminiscent of a modern brown alga. However, no internal structures are present, nor are there any other indications allowing it to be identified with certainty as a body or trace fossil. It is also difficult to interpret it as a sedimentary or diagenetic structure." The matter remains undiscussed and unresolved.

The Hakatai Shale at Alf's pseudofossil mine had also yielded to Seilacher (1956) bilobate bulges that hinted at being organic features; these he referred to *Rusophycus* Hall, 1852 ("cf. *Rusophycus* Billings" [*sic*; p. 165]). Glaessner (1969) took note of these fossils but reserved comment on them because he had not had the opportunity to examine them. *Rusophycus*, however, is

thought to be a trilobite resting trace (cf. Osgood, 1970, p. 303) and a member of the *Cruziana* ichnofacies (Seilacher, 1962, 1964, 1967; see also Osgood, 1975); its identification in the Hakatai Shale must be questioned. (Furthermore, Seilacher, 1970, p. 455, suggested that all such resting traces be combined under the ichnogenic name *Cruziana*.)

Together with C. D. Walcott's pseudofossils (discussed in the section on late Precambrian fossils), the Grand Canyon's supply of imaginary Precambrian invertebrates, tracks, trails, and burrows has been neither monotonous nor at any particular time wanting. Genuine Precambrian trace fossils do confuse those workers who try to analyze Precambrian markings, but at least all of the Precambrian exotica (like Walcott's megafossils) have been demoted to pseudofossils, which should bring some peace of mind to many paleobiologists.

Still, the pseudofossil interpretation of some of the Grand Canyon markings may yet survive reinstitution to organic status; but I make this remark with very cautious enthusiasm. Seilacher (1983) has said that all Vendian Ediacara-type fossils should be reconsidered; among them are the "medusoids" (Seilacher's quotation marks) which "appear as a heterogeneous group of trace fossils and of discoid benthic organisms, rather than as jellyfishes." He summarized:

"Instead of being simply the sigmoidal start of metazoan radiation, the Ediacaran fauna should probably be considered as a distinct, low diversity episode in the evolution of multicellular organisms."

Clearly, the biomechanical architecture of such organisms is in this new perspective completely foreign to paleobiologists. The various Precambrian biotas that cannot be easily ascribed to algal groups may in fact have represented "a widespread, but ultimately failed, biological experiment," and "these creatures were *not* precursors to the great Cambrian explosion of species diversity . . ." (Seilacher, as communicated by Lewin, 1984; *italic emphasis mine*). The implications of this new interpretation are far-reaching, and future studies of all late Precambrian biotas must keep the hypothesis in mind.

A final note should be appended here that pseudofossils of many kinds occur throughout the Grand Canyon stratigraphic section, just as they do in most rock sequences elsewhere. They are sometimes useful in interpreting depositional environments (e.g., McKee's "furoids" and Alf's "vermiform markings"). Paleobiologically, though, they have no direct bearing on the fossil communities in these strata and can be overlooked in this paper.

In Retrospect: Areas of Needed Study

Several areas of Grand Canyon paleontology require either reexamination or more intense study. All areas, of course, can benefit from continued work, but the neglected or understudied ones perhaps must be reintroduced to the research community.

LATE PRECAMBRIAN FOSSILS. Dramatic inroads have been made in Grand Canyon late Precambrian paleobiology in recent years. Forthcoming researches promise to be important both to the understanding of the late Precambrian paleoecology of the Grand Canyon and to late Precambrian paleobiology in general. Intensive research throughout the Grand Canyon Supergroup would be helpful and probably quite rewarding.

PALEOZOIC INVERTEBRATES. Faunal zones in the Grand Canyon have been scrutinized for more than a half century. A few new interpretations on paleoenvironments in some of the formations have been presented. These require careful closer examination if they are to displace the existing interpretations that have been so meticulously laid out by detailed field work. The Devonian strata of the Grand Canyon require the most immediate attention by biostratigraphers. Also, completing the description and analysis of the important collection of brachiopods from the Red-wall Limestone would be a welcome contribution toward understanding the paleoecology of that formation.

PALEOZOIC VERTEBRATES. Although meagerly represented in the Grand Canyon strata, vertebrates are an important group in diagnosing or fine-tuning interpretations of paleoenvironments. More intense field study might benefit interpretations of the Devonian, Mississippian, Pennsylvanian, and Permian strata.

PALEOZOIC TRACE FOSSILS. The relationships between lithologic facies and the benthic paleofauna found in the sediments are beginning to shed light on the value of such analyses in reconstructing small-scale environments of deposition. The good lateral exposures and transitional relationships between various facies of the Grand Canyon strata (in the Kaibab and Toroweap Formations, specifically) is a wide field for more invigorating research.

PENNSYLVANIAN-PERMIAN ICHNOFAUNA. The vertebrate and invertebrate ichnofauna of the Pennsylvanian-Permian strata have not been thoroughly examined since the 1920s. Some evidence has been presented in more recent years that C. W. Gilmore's prolific taxonomic neology is probably unwarranted; many ichnogenera are apparently synonymous, with some physical differences reflecting only the contemporary environment and the temperament of the animals. The Grand Canyon ichnofauna is only one piece in the late Paleozoic ichnite puzzle, of course, and any reexamination must

consider the world picture. Donald Baird has assembled at Princeton University molds of most of the North American late Paleozoic vertebrate ichnotaxa, and they are available to whoever has the ambition and time to begin a restudy of the late Paleozoic vertebrate tracks. Having already in hand such a remarkable collection is certain to save the researcher much time in beginning the study.

LATE PALEOZOIC FLORA. The Grand Canyon's paleoflora is, on the whole, not well understood, nor is the preservation of most of these fossils particularly good. But the Early Permian Hermit Shale flora, in particular, is widely known for its many unique species and specimens. The Hermit flora has been virtually neglected since 1929 and it seems likely that some paleobotanical knowledge can be gleaned from a fresh examination of this material. Most of the species may well remain in uncertain positions in world paleobotany, but a review of them in light of a half century of additional paleobotanical research may improve paleobotanists' perspective of the paleoecologic and paleogeographic significance of unique assemblages in general.

LATE CENOZOIC FOSSILS. In the past decade our knowledge of the late Cenozoic environments of the Grand Canyon region has improved greatly. Recent investigations have pointed to a complex interrelationship of plants, animals, and climate--more complex than previously believed. Lateral (geographic) variances in climato-taxonomic distributions are apparently as significant as vertical (altitudinal) zonations, although not as clearly defined. Furthermore, the response by plant and animal communities to changing environments appears to take place at the species level rather than at the community level. Continued research into these relationships should provide interpretations and applications that will be widely important to biologists in modern and paleontological disciplines. Also, some of the taxonomic relationships of the Late Pliocene(?) mammalian fossils that comprise the Anita local fauna are in need of clarification.

EVOLUTION TODAY. The Grand Canyon is demonstrably a barrier to the migration of some land animals. Taxonomic differences between closely related groups on either side of the Canyon may point to evolutionary divergence. The evolutionary process is probably a slow one by human standards, and it is unlikely that we will perceive real-time evolutionary changes in most species. But the biota of the Grand Canyon region is nonetheless an empirical example of evolution at a small geographic scale, at a resolution that is not well (if at all) discerned in the fossil record. Hypotheses developed at the Grand Canyon could aid studies of the processes and limitations to taxonomic change. Furthermore, evidence for or against Pleistocene backdam flooding of the Grand Canyon will have to be obtained to compose a more complete historical picture of species dispersal in the Grand Canyon region.

PSEUDOFOSILS. Paleontologically unimportant in themselves, pseudofossils can assist in interpreting paleoenvironments. Their usefulness can be more pronounced in studies of Precambrian sedimentary environments where a biota is absent or scarce. The continued identification and classification of pseudofossils of the Grand Canyon Supergroup certainly can help the paleobiologist and sedimentologist in interpreting the late Precambrian environments of the Grand Canyon. Recent suggestions that some Precambrian fossils may represent hitherto unrecognized biologic groups may yet (surprisingly) resurrect some pseudofossils to the world of organic fossils--or at least to the purgatory of the problematica.

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Bibliographical Notes

1. Throughout this paper I have attempted to provide names and dates of taxonomic authorship even where the group is mentioned only casually. This I have done primarily to help other researchers avoid such problems as that which I encountered with *Aelurina* Gill, 1872 (see the section on the Anita local fauna). The sources of the casually mentioned names are not cited in the list of references; doing so would unnecessarily inflate this already lengthy list. If a reader is interested in referring to original sources of taxonomic authorship and subsequent usage, many bibliographical and taxonomic research aids are available; some of the standard references include: *Treatise on Invertebrate Paleontology, Bibliography of Fossil Vertebrates, Nomenclator Zoologicus, Biological Abstracts, Zoologic Record, Bibliography of American Paleobotany, Bibliography and Index of Geology, Bibliography of North American Geology, and Bibliography and Index of Geology Exclusive of North America*. Regarding ichnofossils of invertebrates, Häntzschel (1975, *Treatise on Invertebrate Paleontology*, Pt. W, Suppl. 1) is an outstanding source; for paleobotanical genera, refer to Andrews (1970, U.S. Geol. Survey Bull. 1300).

2. An historical review paper such as this relies on a large number of references. The references cited herein of course include non-Grand Canyon items; but if the worker seeks sources specifically about the Grand Canyon, the search might be made easier by referring to existing bibliographies.

A non-annotated bibliography (Spamer *et al.*, 1981) has been published by the Grand Canyon Natural History Association: *Bibliography of the Grand Canyon and the Lower Colorado River, 1540-1980* (GCNHA Monograph 2). It includes 10 sections covering various aspects of Grand Canyon-Colorado River history and science. Part 3, by Billingsley *et al.* (1981), deals with Grand Canyon geology ("geology" including the paleobiological disciplines) and regional Paleozoic stratigraphy and tectonics.

An annotated bibliography of the geology of the Grand Canyon-proper (Spamer, 1983, 1984) has been published by the Geological Society of America. Appended to this bibliography is an annotated catalogue of Grand Canyon type fossils. It has been published in two volumes: *Geology of the Grand Canyon: An Annotated Bibliography, 1857-1982, with An Annotated Catalogue of Grand Canyon Type Fossils* (GSA Microform Publication 13) and *Geology of the Grand Canyon: An Annotated Bibliography, with An Annotated Catalogue of Grand Canyon Type Fossils. Volume 2. Supplement to the Annotated Bibliography (1857-1983), Supplement and Revisions to the Annotated Catalogue* (GSA Microform Publication 14). In the two volumes, more than 1,150 references have been annotated and 189 species of types have been traced through the literature. Both volumes have

been published on microfiche, a medium that some readers find aesthetically unpleasing. But a bibliography of the geology of a limited geographic area targets a rather small segment of the buying market, and publishing costs today demand fiscal astuteness in order to produce such works; the alternative is to not publish them.

References Cited

Publishing space is expensive; so because 417 references are cited herein, frequently cited journals and organization names are contracted as follows:

| | |
|-----------|---|
| AAPG | American Association of Petroleum Geologists |
| AJS | American Journal of Science |
| CIW | Carnegie Institution of Washington |
| GCNHA | Grand Canyon Natural History Association |
| GCNN | Grand Canyon Nature Notes |
| GSA | Geological Society of America |
| GSAAwP | Geological Society of America Abstracts with Programs |
| GSAB | Geological Society of America Bulletin |
| J. | Journal of . . . or . . . Journal |
| J. Geol. | Journal of Geology |
| J. Paleo. | Journal of Paleontology |
| SMC | Smithsonian Miscellaneous Collections |
| USGS | U.S. Geological Survey |
| USGSPP | U.S. Geological Survey Professional Paper |
| USNMP | U.S. National Museum Proceedings |

Other contractions follow standard conventions of abbreviation. All foreign journals and publications are completely spelled out.

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ADDENDUM

Chesterian "Surprise Canyon Formation"

The unnamed pre-Supai buried-valley deposits of western to central Grand Canyon, discussed in this paper, is a new formation to the Grand Canyon stratigraphic column. The formation has not yet been formally named, although a type locality and a name for the unit have already been selected, and the name approved by the U.S. Geological Survey (Billingsley, verbal commun., 1984). An informal article (Hodge, 1984) describes Billingsley's discovery of the buried valleys, and a generalized stratigraphic column in the article identifies the formation as the "Surprise Canyon Formation." Stevens (1984, p. 11) also mentions this name ("Suprise [*sic*] Canyon Formation"), but in passing and without citation of source. Although these do not constitute formal publication, because they lack a documented type section, they do manifest themselves as instances of "first use." Once the name is made formal through publication of the type section, users will be able to substitute this name for "pre-Supai buried-valley deposits."

In an abstract, Beus & Billingsley (1984) noted that the pre-Supai formation has now been identified throughout most of the Grand Canyon. The formation is noted to occur intermittently from the Bat Tower area, in western Grand Canyon, eastward to Marble Canyon (refer to Fig. 1 in the preceding paper). Channel size decreases eastward. Beus & Billingsley interpreted the lower

strata of the formation as fluvial valley-fill material; the strata "locally yield a moderately diverse flora, including abundant *Lepidodendron* logs" The upper strata, of shallow marine or intertidal deposits, bear "a rich and diverse invertebrate marine fauna including endothyrids of latest Mississippian age." The whole sequence is interpreted as a large east-west estuary system.

Trace Fossils

Seilacher (1970), in placing presumed trilobite trace fossils under the single ichnogenus *Cruziana* d'Orbigny, 1842, described a new species, *C. arizonensis* (Seilacher, 1970, p. 460; figs. 7-8 & 7-9 on p. 458). The type locality is in the upper Tapeats Sandstone along [South] Kaibab Trail. Seilacher reported that other, previously published specimens of *C. arizonensis* appear in Walcott (1918, pl. 39, figs. 1, 3, 4, pl. 41; see also pp. 174-175 [Walcott's "trilobite tracks and trails" from the Tapeats Sandstone]) and in Seilacher (1956, pl. 8, fig. 5; see also p. 163 [Seilacher's *Rusophycus* sp. from the Tapeats]). *C. arizonensis*, placed by Seilacher within his "*semplicata* group," was diagnosed by him as "Mainly resting tracks."

In my Grand Canyon type fossils catalogue, I failed to take note of *C. arizonensis*; so this ichnospecies becomes the 191st taxon in that catalogue. A formal Grand Canyon Type Fossil Number will not be assigned, however, until a

supplement to the catalogue is prepared. (For the record, synonyms of *Cruziana*, according to Seilacher [1970, p. 454], are *Bilobites* d'Orbigny, 1839, and *Rusophycus* Hall, 1852. Seilacher did not mention *C. rustica* White or *C. linnaerossi* White [refer to the preceding paper].)

Early Tertiary Stratigraphy

An abstract by Young & Hartman (1984) takes note of "probable Early Eocene viviparid gastropods" within limestones of "rim gravels" on the Coconino Plateau 30 miles southwest of Grand Canyon. Young & Hartman recorded that "These are the first age-diagnostic fossils collected from these widespread Tertiary sediments previously considered as Pliocene, Miocene, or Oligocene in age." The significance of these fossils, the authors pointed out, is that they can provide controls in dating the problematical late Cretaceous-early Tertiary history of the Grand Canyon region. Prior to the discovery of these fossils, dating was accomplished for the most part by lithologic stratigraphy. This period along the Colorado Plateau margin was one of erosion during the Laramide uplift; it was followed on the southwestern Plateau by a period of fluvial aggradation and lacustrine sedimentation. A better understanding of the age relationships of the regional early Tertiary rocks can improve interpretations of the early drainage history of the region, a history that eventually leads to the development of the Grand Canyon.

Stanton's Cave Paleoenvironments

A monograph on the Stanton's Cave paleoenvironments (Euler, 1984) is now in press. This is an important contribution to studies of late Pleistocene environments in the Grand Canyon. Euler (written commun., 1984) has indicated that this publication also includes a new C^{14} age for the Stanton's Cave driftwood. (The driftwood, as noted in the preceding paper, had before been dated at >35,000 yr BP.) The U.S. Geological Survey has now dated the driftwood at 43,700 \pm 1800 -1500 yr BP. This monograph, Euler stated, also "contains a chapter on the possible damming of the river at Nankoweap although we have no correlatable date for this hypothetical event." There also remains some conjecture among researchers that the river level was already high enough, without invoking dams, to permit driftwood emplacement in the cave. Euler also pointed out that "the lava dam at Toroweap is much too early for the Stanton's Cave driftwood," an obvious point which I did not make clear in the preceding paper. Nonetheless, Stanton's Cave was almost certainly flooded by Lake Balquidder during the Toroweap damming events.

Isolated Habitats

As noted in the preceding paper, some cave-dwelling invertebrates of the Grand Canyon seem to be vestigial populations of forest floor-litter animals stranded by the early Holocene elevation of life zones in the Canyon. Another supporting example was introduced by Triplehorn (1975), wherein the new species of living beetle, *Eleodes* (*Cavernaleodes*) *leptoscelis*, is apparently known only from the Grand Canyon. The three caves that yielded *E. (C.) leptoscelis* are all on the South Rim at an elevation of about 4,500 ft (i.e., in the Redwall Limestone). Triplehorn's new subgenus *Cavernaleodes* is noted by him to be exclusively cave-dwelling. In addition, he noted that *Cavernaleodes* is characterized by "structural modifications which I speculate are associated with a cavernicolous existence" (p. 39). (The type species of *Cavernaleodes* is *E. easterlai* Triplehorn, also a new species, from Texas.)

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★ signifies a new citation for this paper.

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Additional Reference

The following reference was brought to my attention as this paper was going to press. I have not had the opportunity to examine this paper, but it may contain new or revised information on the late Pleistocene environments of western Grand Canyon:

- PHILLIPS, Arthur M., III. 1984. Shasta ground sloth extinction: Fossil packrat midden evidence from the western Grand Canyon. In: Paul S. Martin & Richard G. Klein (eds.), *Quaternary extinctions; a prehistoric revolution*. Tucson: University of Arizona Press, pp. 148-158.